# SPINAL CORD INFLUENCES ON FORELIMB MOVEMENTS INDUCED FROM THE RETICULAR FORMATION

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# CHAPTER I

## INTRODUCTION AND PROBLEM FORMULATION

In recent years, a considerable amount of experimental work has been performed by means of electrical stimulation in order to clarify the functional significance of the reticular formation of the brain stem (2.21). Two main groups of effects have been distinguished from these studies. The first was concerned with modification of cortical and subcortical activity; the second, with modification of muscular activity through the bulb and spinal cord. The subject of this thesis deals specifically with only part of the latter effect, i.e., the forelimb movements which can be elicited by electrical stimulation of the midbrain reticular formation.

This investigation requires a consideration of the nature of the movements obtained, i.e., the flexion or the extension of a joint and of time relationships, i.e., the latencies after which they appear, their speed, and the duration of the effect.

### I - NATURE OF THE MOVEMENTS

In 1905, Thiele (32) described motor responses elicited by electrical stimulation of the tegmentum of the midbrain in decerebrate preparations. These responses con-

sisted of ipsilateral flexion and contralateral extension of the forelimbs, the reverse in the hindlimbs, curving of the neck and trunk concave to the side of the stimulation, and swinging of the hindlimbs in the same direction. This was called the mesencephalic tegmental response.

In 1930, Hinsey, Ranson and Dixon (8) again described this response, in decerebrates, as ipsilateral flexion and contralateral extension of the forelimbs. The hindlimbs were bilaterally flexed and swung to the side of the stimulation. The head and neck turned to the same side. Similar results were reported by Ingram et al. in 1932 (10) by stimulation of the midbrain tegmentum in the intact animal.

In 1946, Magoun and Rhines (12-20) described generalised facilitation and inhibition of cortically or reflexly induced movements, by stimulation of the brainstem reticular formation. Sites which inhibited indifferently flexor or extensor muscles were said to be localised mainly in the medio-ventral part of the medulla oblongata. The facilitatory areas were lateral and dorsal to this mass, and extended rostrally through the pontine and mesencephalic tegmentum as far forewards as the "ventral diencephalon". This phenomenon soon became the basis on which theories of spasticity and rigidity were formulated (25).

In 1953, Sprague and Chambers (31) questioned the validity of the concept of a non-reciprocal motor function of the brain stem reticular formation at least as a true physio-

logical mechanism. They revived the idea of a reciprocal function as earlier suggested by Thiele and Hinsey (32.8), by stimulating normal and decerebrate cats through electrodes implanted into the reticular formation of the medulla oblongata.

Only from a minority of points stimulated did they observe generalised inhibition or facilitation of decerebrate rigidity. The former could be obtained at threshold and at suprathreshold values, but the latter only occurred at high suprathreshold voltages.

Most points yielded reciprocal effects. Medially, from the inhibitory area of Magoun, they obtained ipsilateral flexion and contralateral extension of the forelimbs; laterally, from the facilitatory area, ipsilateral extension and contralateral flexion. The hindlimb behaved as the forelimb of the same side. The trunk was concave to the side of the stimulation and the head turned to the side of the flexed leg. These represent the usual movements but a variety of them was possible especially in the hindlimbs. There were no changes in the movements with changes in frequency. Post-stimulatory reversals were minimal in the formal and maximal in the decerebrate animal. Otherwise normal, decerebrate and even decerebellate cats gave the same response.

Since the movements are the same in these three preparations, they must be mediated by pathways going directly down the bulb into the spinal cord and not up and around a

circuitous route through the diencephalon and the hemispheres or through the cerebellum.

It remains as yet unanswered, however, to what extent the forelimb movements might be dependent upon long propriospinal systems caudal to the brachial segments of the spinal cord. Large cells in the anterior motor horn of the lumbar cord which do not show evidence of retrograde degeneration upon anterior motor root section but which are affected by transection of the cord from C3 to Th12 were originally described by Cooper and Sherrington (3), who believed that they gave origin to the crossed ventral spinocerebellar tract. Sprague found that some of them terminate in the cerebellum in the macaque (27) but failed to find evidence that they were activated by physiological stimulation of end organs and electrical stimulation of nerves in the cat (28). He concluded that they were an ascending component of the bulbospinal tonus regulating mechanism (29). The same author later made a detailed study of the number and distribution of Cooper-Sherrington cells and suggested that they are responsible for the tonic inhibition of the forelimb extensors which is released by thoracic hemisection in decerebrate preparations (30). This had been described and named the Schiff Sherrington phenomenon by Ruch (22, 23). In the cat the Cooper Sherrington fibers have no significant projection to the cerebellum. They are believed to be a

direct pathway to the contralateral cervical segments of the spinal cord for an ascending component of the bulbospinal mechanism influencing muscular tonus in the forelimbs (30).

It would appear that there are two ways in which this or similar propriospinal connections might influence the forelimb movements obtained by reticular formation stimulation. It may be either part of a long multisynaptic pathway activated by the stimulation, or its tonic influence upon the anterior motor horn cells of the cervical region may modify the response of the latter to the stimulation coming from above. That supraspinal effects, at least as far as the phenomenon of facilitation and inhibition is concerned, do not depend as much upon the structure stimulated as on the intrinsic spinal cord organization and the balance of various other influences upon the common motor neuron pool has already been suggested by the experiments of Austin and Emmers (1, 6).

Do long propriospinal pathways ascending from the low thoracic and lumbar cord actually form part of an intrinsic spinal cord organization upon which would depend the sign (flexion or extension) of the forelimb movements obtained by reticular formation stimulation, or expressed differently and with different emphasis, do such fibers form part of a long chained circuitous pathway through which the reticular formation can modify the forelimb movements it can itself elicit from the cervical cord? The present series of experiments was conceived to answer this question.

## II - TIME RELATIONSHIPS OF THE MOVEMENTS

After the publication of Sprague and Chambers which emphasized the reciprocal function of the reticular formation, Gernandt and Thulin (7) re-examined the phenomenon of facilitation and inhibition of reflexes as described by Magoun et al. (12, 20). They confirmed that this particular effect was indeed mostly non-reciprocal, i.e., affecting indifferently flexors or extensors, though they did find a minimal number of points with reciprocal effects.

They also described a "petering out" of the effect of the conditioning stimulus, and they stated that in the 10 seconds period of stimulation, "the facilitatory effect in most cases does not continue throughout the stimulation period but the amplitude diminishes gradually. After such a type of stimulatory facilitation comes a poststimulatory effect usually causing a more or less long depression of excitation over a period of 10 to 60 seconds after the close of the conditioning stimulus". The same holds true for inhibition but with signs reversed. Such an effect may be due to fatigue or depression of the pathways involved or to activation of other pathways opposing stimulation after a long latency.

In 1956, Mihailovic and Delgado (16) published their study on stimulation of the monkey brain with various parameters of stimulation. They described movements from the same points of the cortex or subcortical centers as having a changing quality with changing frequency. At low frequencies, below 30 cps, movements were tremulous at the same frequency as the stimulus. From 30 to 250 cps, tremors and fasciculation were lost and a slow smooth movement appeared. With increasing frequency, responses were more abrupt, with shorter latencies. At the highest frequency of 5000 cps, nothing but a rapid movement in the form of a jerk was obtained at the very onset of the stimulation. Apart from this jerky movement, they did not report any "petering out" of the movements as Gernandt and Thulin (7) had described for the phenomenon of facilitation and inhibition. It is to be noted that Mihailovic and Delgado were stimulating for two seconds periods only and that loss of facilitation had been observed at 7-8 seconds.

The question arises whether the "petering out" effect described by Gernandt and Thulin for the phenomenon of facilitation and inhibition applies to the patterns of movements elicited from the reticular formation. If this is the case, it should be asked whether, for the forelimbs at least, this is in some way due to an opposing influence from the lower thoracic and lumbar cord rather than simply dependent on fatigue

and depression of the pathways involved. The experiments, devised to study the nature of the movements, might also shed some light on this problem.

CHAPTER II

## MATERIAL AND METHODS

The present investigation deals with a series of 10 adult cats in which bipolar platinum electrodes were chronically implanted into the reticular formation of the midbrain.

The area of the midbrain was chosen because:

1- The mesencephalic reticular formation is easy to reach with a vertical electrode without interfering with structures essential to motor function. At the chosen stereotaxic coordinates, the electrode comes down rostal to the cerebellum and the bony tentorium through the occipital lobe and the inferior colliculus.

2- The fibers of the reticular formation, at this level, do not descend to the spinal cord but they must synapse at least once in the pons or the medulla oblongata upon those cells possessing long descending reticulo spinal axons (Brodal 2, Rossi and Zanchetti 21). It is thought that having passed through at least one synapse, the impulse is probably more physiological upon reaching the interneuronal pool in the gray matter of the cord.

It was intended to place the electrodes in that part of the reticular formation which has been called the nucleus cuneiformis by Olszewski (18). This nucleus occupies the area

ventral to the corpora quadrigemina in the dorsal part of the tegmentum. (Fig. 1). It extends from the caudal pole of the inferior colliculus to the rostral border of the superior colliculus. Its principal relations are the central gray medially, the corpora quadrigemina dorsally and the medial lemniscus laterally. Ventrally it must be distinguished from the nucleus subcuneiformis. This is done on the basis of cell characteristics. The nucleus cuneiformis is composed of small and medium sized, triangular or fusiform cells with a centrally placed nucleus and scanty Nissl substance. The cells lie with their long axis directed dorsomedially and are associated with numerous glial satellites. The nucleus subcuneiformis presents a similar picture but can be distinguished by the presence of a few large cells, some of which have an eccentric nucleus and peripherally arranged Nissl granules, and by a lesser degree of cellularity and of glial satellitosis. By keeping to the medial side or to the center of this nucleus, the exposed tip of the electrode would be clear of the red nucleus, the brachium conjunctivum decussation, the substantia nigra and corticospinal fibers, and finally of the medial lemniscus.

The electrodes were 0.1 mm. in diameter with an exposed tip 1 mm. in lenght and an interelectrode distance of 0.75-1.0 mm. The two platinum wires were insulated in separate glass capillaries and they were held together and to a metal

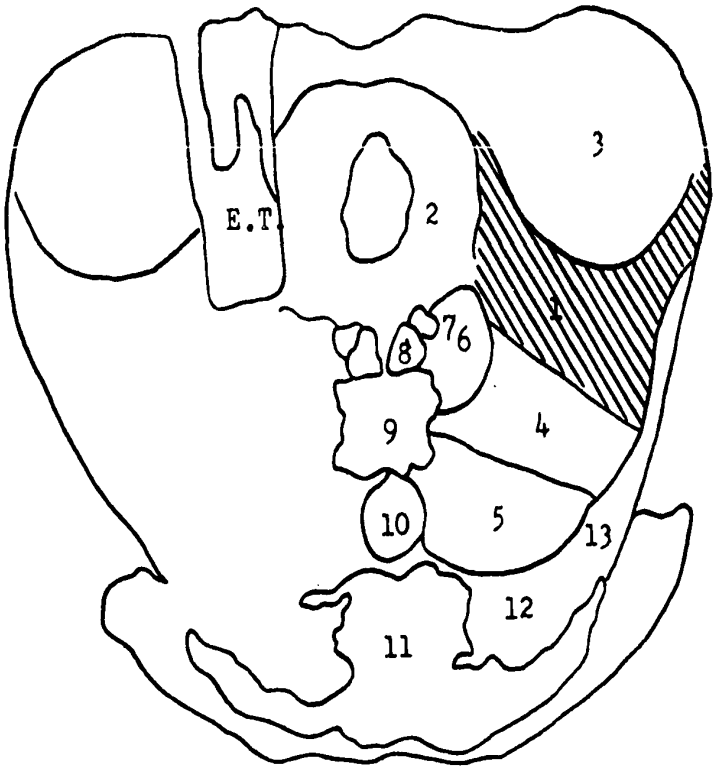



Fig.1 The nucleus cuneiformis at the level of n.IV in the cat, modified from Olszewski's diagram of the human brainstem. The position of the electrode tract is similar to that found in CATS #XXVII, XXV, XXIII, XXII, and XXI.

1. Nucleus cuneiformis.
2. Griseum centrale mesencephali.
3. Nucleus colliculi inferioris.
4. Nucleus subcuneiformis.
5. Nucleus tegmenti pedunculopontinus.
6. Tractus tegmenti centralis.
7. Nucleus nervi trochlearis.
8. Fasciculus longitudinalis medialis.
9. Decussatio pedunculorum cerebellorum superioris.
10. Nucleus interpeduncularis.
11. Griseum pontis.
12. Pes pedunculi.
13. Lemniscus medialis.

E.T. Electrode tract.

rod by ordinary sealing wax. The rod was fixed to the stereotaxic holder and the electrode was introduced into the brainstem through a burr hole in the skull. The site of implantation was at the frontal plane 0 or 1 plus of the Horsley Clarke cooordinates, 2.5 mm. from the midline. The stereotaxic atlas of Jasper and Ajmone-Marsan was used for this orientation, (11). The depth was determined by the length of the prefabricated electrode, usually 18 mm. The electrode was lowered into the brain until the sealing wax touched the dura and was then fixed in the burr hole with dental cement. Touching the metal rod with a soldering iron readily released it from its sealing wax attachment. Two insulated wires led from the electrodes to a small socket imbedded in a plexiglass headdress over the closed skin incision.

Stimulations were started on the second postoperative day. The cats were lightly anaesthetized with 0.5 cc. of a 5% solution/Kg of Nembutal given intraperitoneally and suspended in a specially constructed hammock. (Fig. 2). If struggling was still present at this level of anaesthesia, the dose was increased by additions of 0.5 cc. until the cat lay quietly in the sling. Pinch reflexes were always present in the four limbs during the experiment. The head usually drooped and was supported in a separate sling.

The stimulations were carried out on three separate days. Unipolar square waves were obtained through a Grass Stimulator model S4D coupled with a Stimulus Isolation Unit

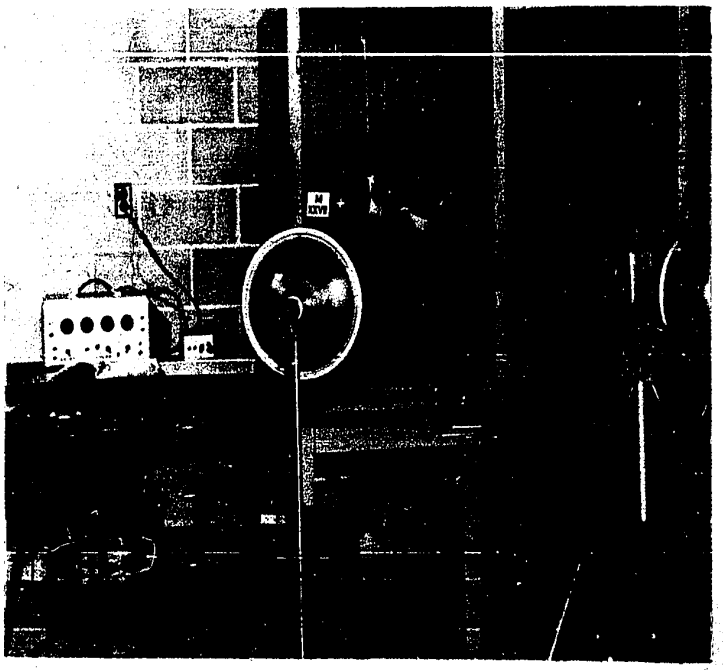


Fig.2 Equipment used for the study of patterns of movement.

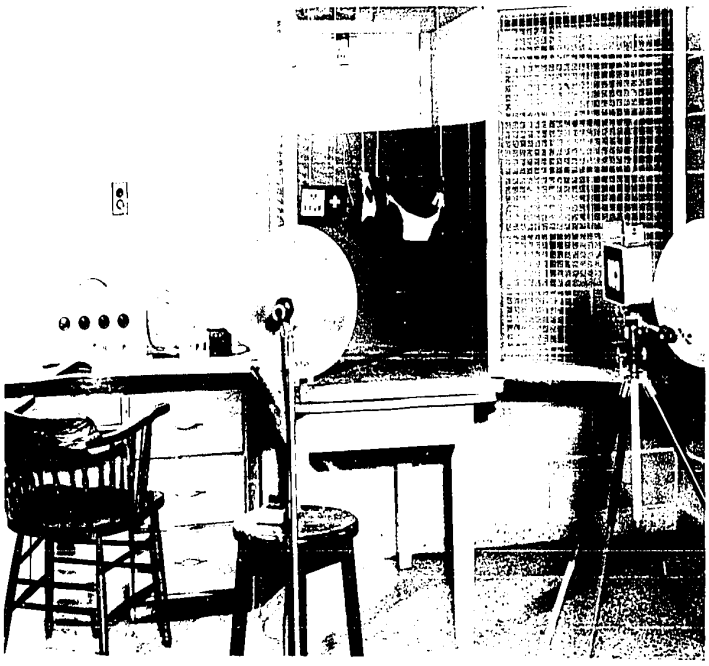


Fig.2 Equipment used for the study of patterns of movement.

model SIU-4B. The positive pole was shifted from one to the other electrode at each stimulation. An interval of 2 (occasionally 3) minutes was present between the beginning of each stimulation. The latter lasted 20 seconds.

The usual parameters of stimulation were of the order of 500 cps with an impulse duration of 1 msec., and of 50 cps with an impulse duration of 5 msec. The frequencies yielding typical changes in the time relationships of the movements were chosen. The impulse duration was determined according to Mihailovic and Delgado (16) who showed thresholds for movements from subcortical areas to be at their lowest at impulse durations of 1.0-5.0 msec. 1.0 msec. was the maximum duration possible with the stimulator of 500 cps. Since threshold diminishes with increasing frequency and pulse duration, 5.0 msec. was used with 50 cps to render the thresholds at both frequencies more comparable.

Stimulations were started at 0.5v. and increased with 0.5v. increments until a fully developed movement obtained, and even a few steps beyond this level. This was not always possible, for a prohibitively violent movement was sometimes seen before or just at the appearance of the complete movement. Moreover, whether the movement was complete or incomplete, violent or moderate, increases in voltage were not pursued higher than 2.5-3.0v. above the forelimb threshold.

A postbrachial section of the spinal cord was then performed at the level of Th3 or Th4, on six of the ten cats. The operations were made under Nembutal anaesthesia. The spinal cord was exposed by removing the spinous process and laminae of the 3rd or the 4th thoracic vertebra. It was then raised away from the body of the vertebra and completely severed.

Stimulations, with observations and recordings, were again carried out on 2 or 3 separate days, as before the lesion.

The animals were then sacrificed and microscopic sections of the midbrain were cut and stained with Cresyl Echt Violet for cells and Heidenheim for fibers, to determine the exact site of the lesion.

METHOD OF RECORDING

I - The nature of the movements

It became at once apparent that it would not be sufficient to describe the movements in terms of flexion or extension of one or the other limb. Indeed the most common movements observed were more complex than expected and consisted in a combination of flexed and extended joints in the same limb. It was therefore necessary to keep records of all joints. The following system of notation was used.

IF refers to the ipsilateral forelimb.

CF refers to the contralateral forelimb.

#1, 2, 3, 4, refer to the shoulder, elbow, wrist and toes respectively.

f indicates flexion; e indicates extension.

Anteflexion and retroflexion of the shoulder are considered as extension and flexion respectively.

Thus IF f12e34 describes a movement of the ipsilateral forelimb consisting of flexion (retroflexion) of the shoulder and elbow, and extension of the wrist and toes.

Hindlimb movements in the "normal" unoperated cats are irrelevant to this investigation because they are absent after the postbrachial sections. They are therefore not reported except to note their presence and their tresholds relative to the forelimbs.

Two frequent patterns of movement require a word of explanation.

1) CF e1234: Because of a slight internal rotation of the forelimb when it hangs in the hammock, extension of the elbow usually brings about an apparent abduction. It is evident however that a true abduction of the limb from the

shoulder is sometimes obtained (especially when associated with flexion of the elbow). It has not been attempted to distinguish between a true and an apparent abduction in the case of an extended elbow. All are recorded as equal.

2) IF f12e34: Because of the same internal rotation of the forelimb, flexion of the elbow often tends to bring the paw close to or past the midline. This adduction is not as marked as the abduction described above and though always present has usually not been recorded because it was negligible.

Three types of patterns will be described.

i) A simple movement is one in which all joints give the same movement: flexion or extension.

ii) A composite movement is one in which at least one joint behaves differently from the others.

iii) A compound movement is one in which at least one of the joints has a movement reversal, i.e., flexion to extension, or vice-versa, before cessation of stimulus. This is usually seen at voltages above threshold.

N.B. A fully developed movement is one in which all joints show movement.

II - The time relationships

At the two most employed frequencies, very different time relationships were seen. At a frequency of 50 cps and a duration of 5 msec. (50:5), the movements usually begin after

a variable latency and proceed slowly to increase in size until a maximal amount of development is reached. This maximal development is maintained for the full time of stimulation and upon cessation of the stimulus the limb falls back to its original "normal" position. A maximally developed movement is either a fully or an incompletely developed movement in which the joints involved have reached the maximal intensity of movement (in time).

At a frequency of 500 cos, and a duration of 1 msec. the movements usually appear suddenly without latency and increase in size abruptly to reach a maximal development almost immediately. They are however not maintained in this position for the full time of stimulation but begin to peter out slowly, sometimes returning to the original position before, sometimes only after the end of stimulation.

Four timings were recorded during the movement of both forelimbs at both frequencies mentioned. The values reported represent averages of the recordings on the two or three days of stimulation.

i) Latency: The time elapsed between the onset of stimulation and the initiation of the movement.

ii) Maximum: The time, from the onset of stimulation, at which the movement of a limb has reached its maximal development.

iii) Time of effect (T.E.): The time, from the onset of stimulation, at which the maximally developed movement

begins to peter out.

iv) Normal (N.): The time, from the onset of stimulation, at which the limb is completely back to its original "normal" position.

These timings are very gross and were determined according to the seconds hand of a wrist watch. Below 5 seconds they are correct within plus or minus ½ second, but above 10 seconds they may vary by plus or minus 2 seconds. At values around 10 seconds therefore, changes observed in the time relationships after the lesion, must vary by at least 5 seconds to be of any significance.

Cinematographic records were taken of all cats (except #XX) on 8 mm. Kodachrome type A colour film, on one, two or three separate days as reported for each cat.

# CHAPTER III

## RESULTS

CATS #XXIII, XXII, XXI and XX.

Stimulations performed only in

"normal", intact animals

without cord lesions.

CAT #XXIII

Weight: 6½ lbs.

Electrode implantation: Dec. 14, '59

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 17 mm.

Stimulation experiments: Dec. 16, 18, 21.

Cinematographic records: Dec. 16 and 18.

Site of electrode: The exposed tip of the electrode was mainly within the nucleus cuneiformis, at the level of the oral pole of n.IV. It encroaches slightly upon the central gray medially and upon the nucleus of the inferior colliculus laterally. (Fig. 3).

## RESULTS

A - Forelimbs

At 500:1, on Dec. 16, the fully developed movement appeared at 4.5v. in the form of IF f12e34 and CF f12e34 with abduction. The threshold for the forelimbs was 4.0v., and yielded IF f2 and an ill-defined CF abduction. On Dec. 18, the fully developed movement was present at 3.0v. The threshold at 2.0v. yielded an ill-defined CF abduction. On Dec. 21, the fully developed movement was present at 3.0v. The

threshold at 2.5v. yielded IF f2. The maximum voltage used on the three days were those at which the fully developed movement appeared.

There were no latencies. The maximal development occurred within 1 second and began to peter out after 5 to 10 seconds. The limbs were back to normal before the end of the stimulation at threshold (10 to 16 sec. in CF and IF respectively). At 0.5v. above threshold, they fell back to normal only 4 seconds after cessation of the stimulus.

At 50:5, on Dec. 16, the fully developed movement appeared at 4.5v. in the form of IF f12e34 and CF f12e34 with abduction. The threshold was at 2.5v. and yielded CF abduction. On Dec. 18, the fully developed movement appeared at 3.0v. The threshold at 2.5v. yielded CF abduction with IF f12. On Dec. 21, the fully developed movement was at 4.5v. The threshold at 3.5v. yielded CF f2 with abduction and IF f12. The maximum voltage used on the three days was 0.5v. above that required for the fully developed movement. It should be noted that at threshold, it was sometimes difficult to decide whether the movement consisted of extension or flexion in the contralateral elbow. Its obvious though slight flexion at higher voltages made us decide to record it as a flexion, although the general movement of the limb at both frequencies was more similar to the usual f1e234 with abduction found in the contralateral forelimb than to the IF f12e34 found in the ipsilateral forelimb. (see CAT #XXV, fig.20).

On the first two days, there were latencies of 1 to 2 seconds at threshold which disappeared at 0.5v. above threshold. The maximal development occurred at 7 to 8 seconds in both limbs at threshold. It rapidly decreased to 2 seconds in CF at 0.5v. above threshold, while it remained as high as 5 seconds in IF at 1.0v. above threshold. The movement was well maintained for the full time of stimulation except at 1.0v. above threshold in CF where it began to peter out at 12 seconds. The CF fell down to normal within 1 second after cessation of the stimulus but IF came down very slowly and was not "normal" until 5 to 10 more seconds. On Dec. 21, however, all these time relationships were disrupted. There were no latencies; the limb reached its maximal development within 1 second after the onset of the stimulus; the movement was well maintained for the full time of the stimulation and fell to normal within one second after cessation of the stimulus.

B - Head movements

On the three successive days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted, and the head turned contralaterally at both frequencies. Thresholds were lower than for the forelimbs.

C - Other movements

i - Hindlimb movements appeared at threshold values greater than those of the forelimbs.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - There were no tail movements.

iv - The body did not turn.

v - Occasional urination was recorded.

vi - Shivering and coarse tremors were present in all limbs within one half hour after the beginning of the stimulation session. They were arrested during the actual stimulation even at subthreshold values.

vii - There were no moanings during the stimulations.

Fig.1 Site of electrode in midbrain of CAT #XXIII

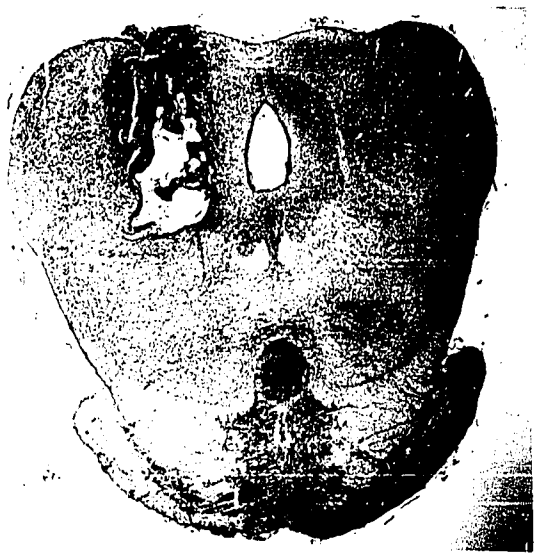


Fig.3 Site of electrode in midbrain of CAT #XXIII

CAT #XXII

Weight: 6½ lbs.

Electrode implantation: Nov. 30, '59.

Stereotaxic coordinates: Frontal plane 1, 2.5 mm. to the right of the midline.

Depth of the electrode: 18 mm.

Stimulation experiments: Dec. 2, 3.

Cinematographic records: Dec. 2.

Site of electrode: The exposed tip of the electrode was situated mainly within the nucleus cuneiformis, at the level of the caudal pole of n.IV. It encroaches slightly upon the central gray medially and the nucleus of the inferior colliculus laterally. (Fig. 4).

## RESULTS

A - Forelimbs

At 500:1, on Dec. 2, the fully developed movement appeared at 3.5v. in the form of IF f12e34 and CF f1e234 with abduction (see cat #XXV, fig. 20). The threshold for the forelimbs was 2.5v. and yielded IF f12 and CF e2 with abduction. The maximum voltage used was 1.5v. above that required to obtain a fully developed movement. On Dec. 3, the fully developed movement appeared at 3.0v. (the maximum voltage used). The threshold at 2.0v. yielded IF f12.

There were no latencies. The maximal development occurred at 2 seconds at threshold, but was within 1 second after a 0.5v. increase. It began to peter out at 8 seconds in both limbs, IF often preceding CF. This time was shortened with increasing voltage. The limbs were back to their original position only after cessation of the stimulus, usually within 1 second.

At 50:5, on Dec. 2, the fully developed movement appeared at 5.0v. in the form of IF f12e34 and CF f1e234 with abduction. The threshold was 3.0v. and yielded CF e2 with abduction. On Dec. 3, the fully developed movement appeared at 4.0v. The threshold at 3.0v. yielded IF f12 and CF e2 with abduction. The maximum voltage used were those required to obtain a fully developed movement.

Latencies of about 5 seconds were present in both limbs at threshold (Chart #VI, a). These latencies disappeared in IF upon raising the voltage by 0.5v., but persisted in CF, though diminished, until the voltage had been increased by 1.5v. The movement reached its maximal development in both limbs at 10 seconds at threshold, but this time was steadily decreased with increasing voltage and it was finally within one second at 1.5v. above threshold. This position was well maintained for the full time of stimulation at threshold and 0.5v. above threshold. At 1.0v. and 1.5v. above threshold, however, it began to peter out after 15 seconds. The limb fell

back to its original position within one second after cessation of stimulus at all voltages in both limbs.

B - Head movements

On the two days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned ipsilaterally at both frequencies. On the first day poststimulatory reversals were present at 50:5. Occasional contralateral head turns were also observed at this frequency. Threshold were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at threshold values higher than those of the forelimbs.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - The tail went up and to the right.

iv - The body curved with the concavity ipsilaterally.

v - Urination was recorded on Dec. 2 only.

vi - Shivering and coarse tremors were present in all limbs within one half hour after the beginning of the stimulation session. They were arrested during the actual stimulation period even at subthreshold values.

vii - There were no moanings during the stimulations.

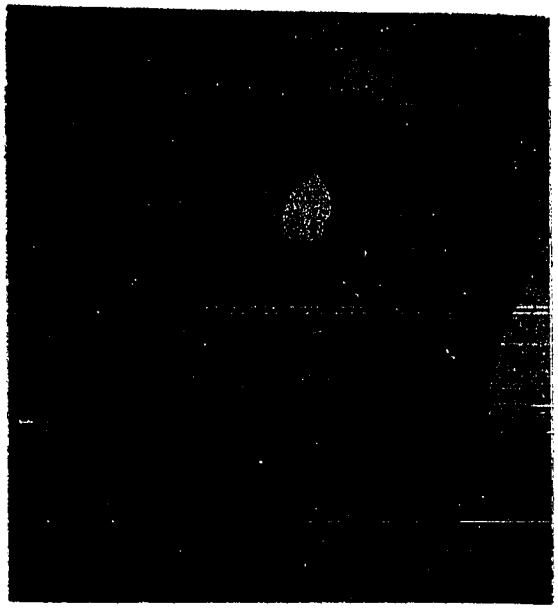


Fig.4 Site of electrode in midbrain of CAT #XXII

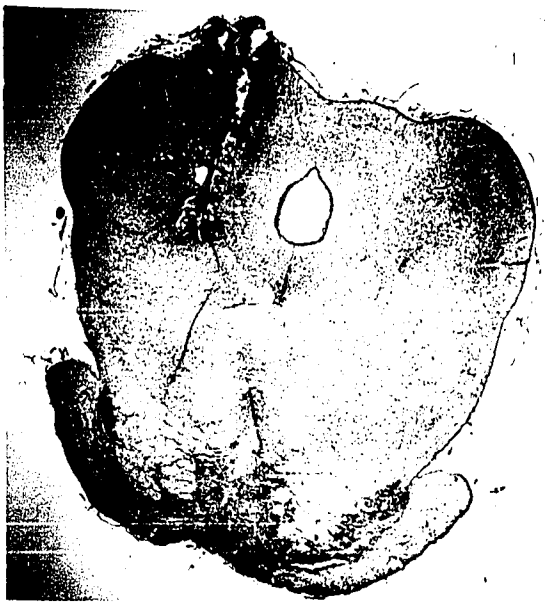


Fig.4 Site of electrode in midbrain of CAT #XXII

CAT #XXI

Weight: 7 lbs.

Electrode implantation: Nov. 16, '59.

Stereotaxic coordinates: Frontal plane 1.5, 2.5 mm. to the right of the midline.

Depth of electrode: 18 mm.

Stimulation experiments: Nov. 18, 19, 20.

Cinematographic records: Nov. 20.

Site of electrode: The very end of the exposed tip of the electrode enters the nucleus cuneiformis at the level of the caudal pole of n.IV. The rest of the tip encroaches considerably upon the central gray medially, and the nucleus of the inferior colliculus laterally.

## RESULTS

### A - Forelimbs

At 500:1, on Nov. 18, the fully developed movement appeared at 3.5v. in the form of IF elf2e34. CF gave no movement. The threshold was 2.5v. and yielded IF f2. The maximum voltage used was 4.5v. On Nov. 19, the fully developed movement appeared at the threshold value of 2.5v. in the form of IF elf2e34. At 3.0v. however, this movement was changed to IF f12e34. CF gave no movement. On Nov. 20, the fully developed movement appeared at the threshold value of 2.5v. in the

form of IF e1f2e34 which became IF f12e34 at 3.0v. At this voltage CF now appeared as f1e234 with abduction. The maximum voltage used on the last two days was 3.0v.

Only the time relationships of IF can be given because of the scanty data on CF. There was a 1 second latency at threshold which readily disappeared at 0.5v. above threshold. The movement was maximally developed at 2 seconds at threshold, but this time was shortened to within 1 second at 1.0v. above threshold. This position was well maintained for 13 seconds at threshold but petered out after 8 seconds from 0.5v. to 2.0v. above threshold. The limb fell to its original position within 1 second after cessation of the stimulus.

At 50:5, on Nov. 18, the fully developed movement appeared at 4.0v. in the form of IF f12e34. CF gave no movement. The threshold was 3.5v. and yielded IF f2. On Nov. 19, the fully developed movement appeared at 3.5v. in the form of IF f12e34, and CF f1e234 with abduction. The threshold was 3.0v. and yielded IF f2 and CF e2 with abduction. On the 20th, the fully developed movement appeared again with stimulation at 3.5v. in the form of IF f12e34 and CF f1e234 with abduction. The maximum voltage used was 4.0v., 3.5v., and 4.0v. on the three successive days.

There were latencies of 4 and 2 seconds in IF and CF respectively at threshold. The CF latency disappeared with a voltage increase of 0.5v. The IF latency persisted at a value

of 1 second even at 1.0v. above threshold. The maximal development was reached at 8 and 4 seconds in IF and CF respectively at threshold, quickening in each with increasing voltage. This position was well maintained for the full time of stimulation at threshold, but began to peter out earlier (16 sec.) in IF at 0.5v. - 1.0v. above threshold.

B - Head movements

On the three successive days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned ipsilaterally at both frequencies. Poststimulatory reversals occurred on the first two days at 50:5 and on the first day only at 500:1. Thresholds were lower than those of the forelimb.

C - Other movements

i - Hindlimb movements appeared at thresholds higher than those of IF. The ipsilateral hindlimb however had thresholds lower than the contralateral forelimb.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - The tail went up and to the right.

iv - The body did not curve.

v - Urination was occasionally observed.

vi - Shivering and coarse tremors were present in all

limbs within one half hour after the beginning of the stimulation session. They were arrested during the actual stimulation even at subthreshold values.

vii - There were no moanings during the stimulations.

CAT #XX

Weight: 6½ lbs.

Electrode implantation: Nov. 16, '59.

Stereotaxic coordinates: Frontal plane 1, 2.5 mm. to the right of the midline.

Depth of electrode: 17 mm.

Stimulation experiments: Nov. 11 and 12.

Cinematographic records: nil.

Site of electrode: The exposed tip of the electrode was implanted laterally in the depth of the nucleus of the inferior colliculus at the periphery of the section. It reaches a group of cells ventral to this nucleus and lateral to the lateral lemniscus, which can be seen at this level, bending medially towards the inferior colliculus. That group of cells seems to correspond in the cat to the nucleus sagulum described in man by Olszewski. This obtains at a level caudal to n.IV in the region of the nucleus coeruleus.

## RESULTS

A - Forelimbs

At 500:1, a fully developed movement was never obtained at the voltages used. On Nov. 11, IF f12 and CF e12 with abduction appeared at the threshold value of 9.0v. The

same obtained up till the maximum voltage used, i.e., 12v. On Nov. 12, only IF f12 was present at the threshold value of 11v. CF e12 was not observed until the maximum voltage used, i.e., 15v.

Only the time relationships of the IF can be given because of limited data on CF. Latencies of 4 to 5 seconds were present. They were followed within another second by the maximal development of the movement. This was well maintained for the full 20 seconds of stimulation. The limb fell back to normal within 3 seconds after cessation of the stimulus.

At 50:5, a fully developed movement was never obtained at the voltages used. On Nov. 11, IF f12 and CF e12 with abduction appeared at the threshold value of 10v. The same obtained till the maximum voltage used, i.e., 14v. On Nov. 12, IF f12 appeared at the threshold value of 13v. CF e12 was not observed until the maximum used, i.e., 15v.

There were latencies of 4 seconds in IF and of 8 seconds in CF. The maximal development followed within 2 to 3 more seconds and was well maintained for the 20 seconds of stimulation. The limbs fell back to normal within 2 to 5 seconds after cessation of stimulus.

B - Head movements

On the two days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned ipsilaterally at both frequencies. There were no

poststimulatory reversals. Thresholds were the same as for the forelimbs.

C - Other movements

i - Hindlimb movements appeared at threshold higher than those of the forelimbs.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - The tail went up and to the right.

iv - The body curved with the concavity ipsilaterally.

v - Urination was not observed.

vi - Shivering or coarse tremors were not observed.

vii - There were no moanings during the stimulations.

CATS #XXVII, XXVI, XXV,

XXIV, XIX and XVIII.

Stimulations performed before

and after the postbrachial sections.

CAT #XXVII

Weight: 7 lbs.

Electrode implantation: Feb. 22, '60.

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 18 mm.

Stimulations of the "normal" cat: Feb. 24, 25, 26.

Postbrachial section: Feb. 29. Level of Th.4.

Stimulations after the cord section: March 1, 2, 3.

Site of electrode: The exposed tip of the electrode was situated mainly within the nucleus cuneiformis at the level of the caudal pole of n.IV. It encroaches slightly upon the central gray medially and the nucleus of the inferior colliculus laterally.

RESULTS

1. The "normal" cat.

A - Forelimbs

At 500:1, on Feb. 24, the most complete movement obtained, appeared at 2.5v. in the form of IF f12 and CF fle234 with abduction. The threshold was 2.0v. and yielded CF fle234 with abduction. The maximum voltage used was 3.5v. On Feb. 25, the same nearly complete movement was present from

the threshold value of 2.5v. to the maximum voltage used (4.0v.). Results obtained on Feb. 26, with a wider range of frequencies are reported separately at the end of this chapter.

There were no latencies. The maximal development occurred within 1 second after the onset of the stimulus. It began to peter out from 13 to 15 seconds later in both limbs (Fig. 9, 10, 11). The limbs were back to their original position only after cessation of the stimulus, usually after a few seconds.

At 50:5, on Feb. 24, the most complete movement obtained, appeared at the threshold value of 3.0v. in the form of IF f12 and CF f1e234 with abduction. The maximum voltage used was 3.5v. On Feb. 25, the same movement appeared at 3.5v. (the maximum voltage used). The threshold was 3.0v. and yielded only CF e2 with abduction.

Latencies of 3 and 2 seconds were present at threshold and 0.5v. above. The movement reached its maximal intensity in both limbs at 10 seconds and was well maintained in this position for the full time of stimulation (Fig. 6, 7). The limb fell slowly back to normal, returning to its original position at approximately 10 seconds after cessation of the stimulus.

B - Head movements

On the three days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the

head turned to the contralateral side. The thresholds were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at thresholds higher than those of the forelimbs.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - The tail went up and to the right.

iv - The body curved with the concavity ipsilaterally.

v - Urination was occasionally observed.

vi - Shivering or coarse tremors were not observed.

vii - Moanings were present at each stimulation.

2. After the cord section.

A - Forelimbs

At 500:1, on March 1, the most complete movement obtained, appeared at 5.5v., in the form of IF fl2 and CF elf2. The threshold was 5.0v. and yielded CF elf2. The maximum voltage used was 6.0v. On March 2, the only movement obtained was IF fl2 at a threshold value of 7.0v. The maximum voltage used was 12.0v. On March 3, the movements were again as on March 1.

There were no latencies and the maximal development occurred within one second after the onset of the stimulation. It began to peter out at 10 seconds and was back to normal at

18 seconds at threshold and one second after cessation of the stimulus at 0.5v. above threshold.

At 50:5, on March 1, the most complete movement obtained, appeared at 6.0v. in the form of IF fl2 and CF elf2. (Fig. 8). The threshold was 5.5v. and yielded only CF elf2. The maximum voltage used was 8.0v. On March 2, no stimulations were made at this frequency. On March 3, the movements were essentially as described on March 1.

Both forelimbs had a latency of 4 seconds at (and 0.5v. above) threshold. This fell to two seconds from 1.0 to 2.0v. above threshold. The time for the maximal development was 10 seconds at (and 0.5v. above) threshold and was shortened to 6 seconds from 1.0 to 2.0v. above threshold. This position was maintained for the full 20 seconds of stimulation. The limb regained its original position within 1 second after cessation of stimulation at threshold but required 5 seconds at higher voltages.

B - Head movements

The pupils dilated, the eyelids and the nictitating membranes retracted, and the head turned contralaterally on both days and at both frequencies.

C - Other movements

All disappeared except the tongue movements.

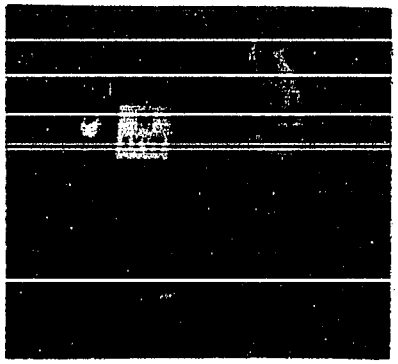


Fig.5 CAT #XXVII Normal
Original position
Feb.24 '60

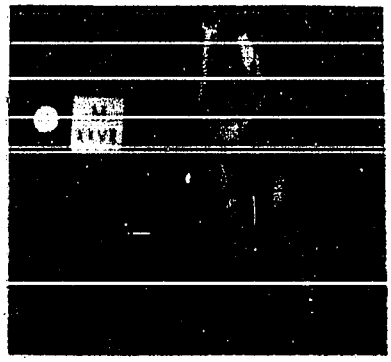


Fig.6 CAT #XXVII Normal
Stimulation: 50:5 3.5v.
Feb.24 '60
Notice extension of the elbow, wrist and toes and abduction of the contralateral forelimb; elevation of the paw of the ipsilateral forelimb consequent to flexion of the shoulder and elbow. Maximal development at 14 seconds.

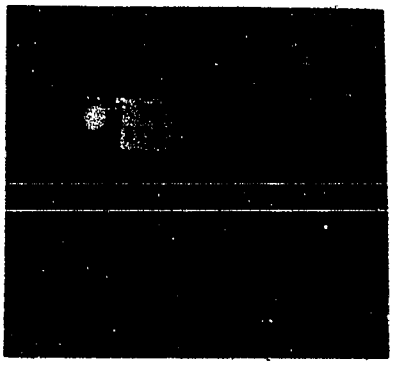


Fig.7 CAT #XXVII Normal
Stimulation: 50:5 3.5v.
Feb.24 '60
Exactly the same position as fig.6 at the 20th second of stimulation. There is no petering out of the movement.

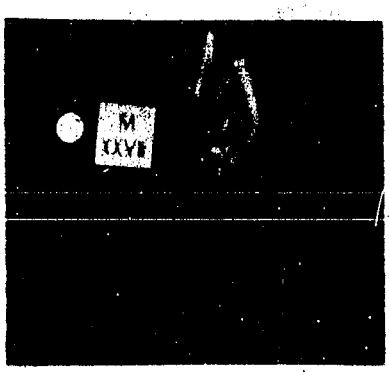


Fig.8 CAT #XXVII Lesion
Stimulation: 50:5 12.0v.
March 1 '60
Notice the change in the movement of the contralateral forelimb: the shoulder is extended and the elbow flexed. There is no change in the ipsilateral forelimb.
Maximal development at 9 seconds

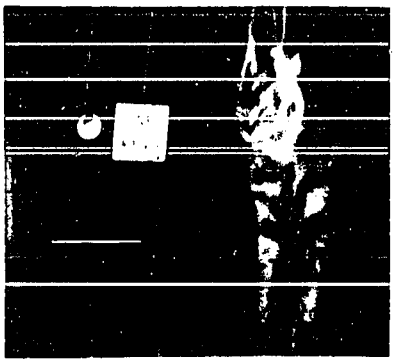


Fig.5 CAT #XXVII Normal
Original position
Feb.24 '60

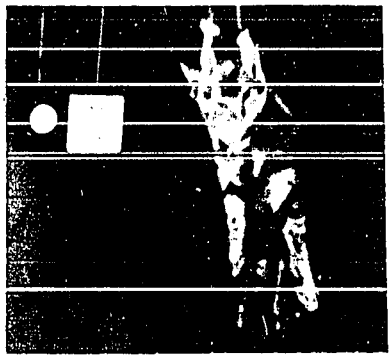


Fig.6 CAT #XXVII Normal
Stimulation: 50:5 3.5v.
Feb.24 '60
Notice extension of the elbow, wrist and toes and abduction of the contralateral forelimb; elevation of the paw of the ipsilateral forelimb consequent to flexion of the shoulder and elbow.
Maximal development at 14 seconds.

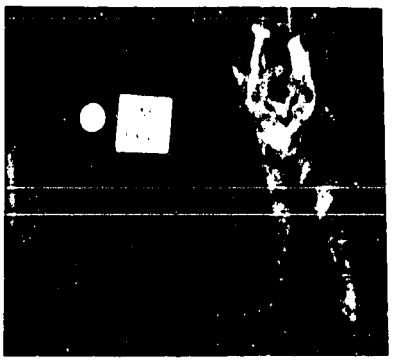


Fig.7 CAT #XXVII Normal
Stimulation: 50:5 3.5v.
Feb.24 '60
Exactly the same position as fig.6 at the 20th second of stimulation.
There is no petering out of the movement.

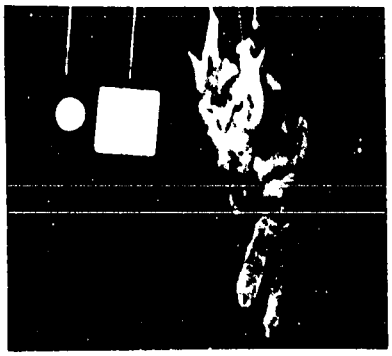


Fig.8 CAT #XXVII Lesion
Stimulation: 50:5 12.0v.
March 1 '60
Notice the change in the movement of the contralateral forelimb: the shoulder is extended and the elbow flexed. There is no change in the ipsilateral forelimb.
Maximal development at 9 seconds

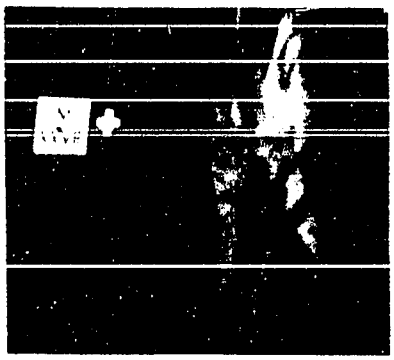


Fig.9 CAT #XXVII Normal
Stimulation: 500:1 3.0v.
Feb.24 '60
Notice extension of the elbow, wrist and toes and abduction of the contralateral forelimb; elevation of the paw of the ipsilateral forelimb consequent to flexion of the shoulder and elbow. Maximal development within 12 seconds.

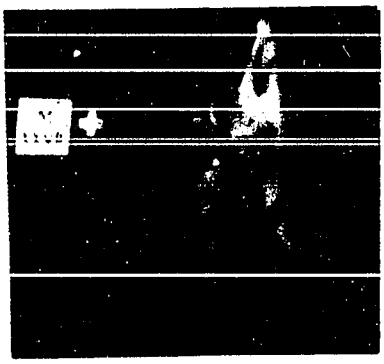


Fig.10 CAT #XXVII Normal
Stimulation: 500:1 3.0v.
Feb.24 '60
Same movement as fig.9 with slight petering out of the movement at 13 seconds.

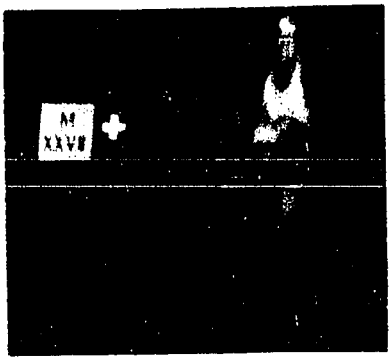


Fig.11 CAT #XXVII Normal
Stimulation: 500:1 3.0v.
Feb.24 '60
Further petering out of the movement at 20 seconds

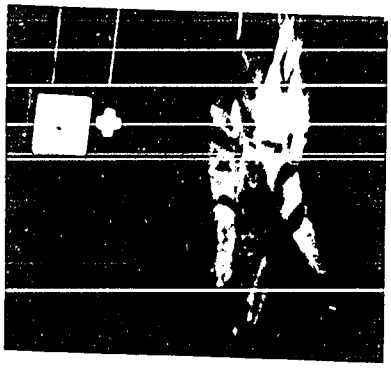


Fig.9 CAT #XXVII Normal
Stimulation: 500:1 3.0v.
Feb.24 '60
Notice extension of the elbow, wrist and toes and abduction of the contralateral forelimb; elevation of the paw of the ipsilateral forelimb consequent to flexion of the shoulder and elbow. Maximal development within 1½ seconds.

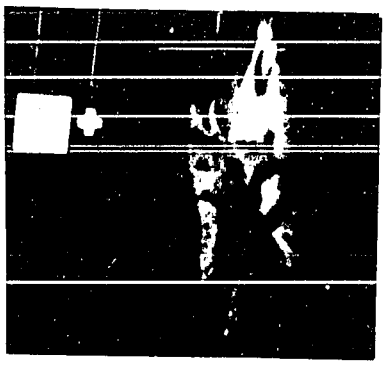


Fig.10 CAT #XXVII Normal
Stimulation: 500:1 3.0v.
Feb.24 '60
Same movement as fig.9 with slight petering out of the movement at 13 seconds.

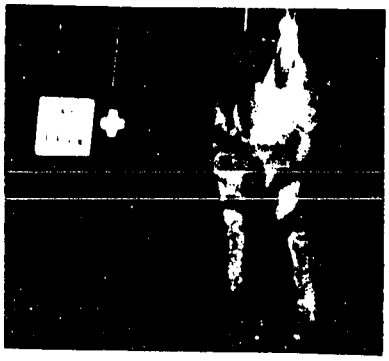


Fig.11 CAT #XXVII Normal
Stimulation: 500:1 3.0v.
Feb.24 '60
Further petering out of the movement at 20 seconds

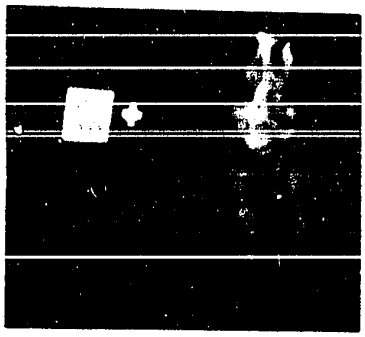


Fig.12 CAT #XXVII Normal
Stimulation: 5000:0.1 3.0v.
Feb.26 '60
Same movement as at 500:1,
fig.9.
Maximal development
within ½ second.

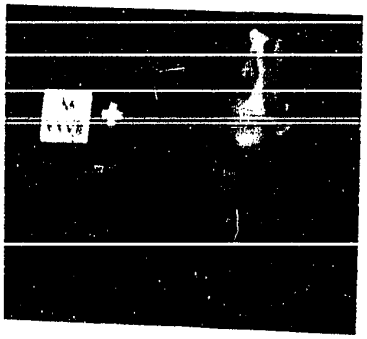


Fig.13 CAT #XXVII Normal
Stimulation: 5000:0.1 3.0v.
Feb.26 '60
Notice marked petering
out of the movement
within ½ second.

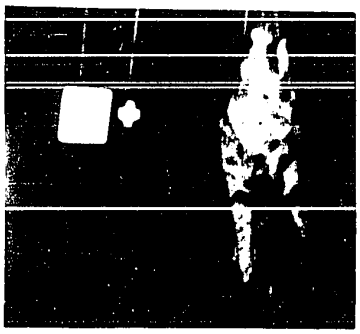


Fig.12 CAT #XXVII Normal
Stimulation: 5000:0.1 3.0v.
Feb.26 '60
Same movement as at 500:1, fig.9.
Maximal development within ½ second.

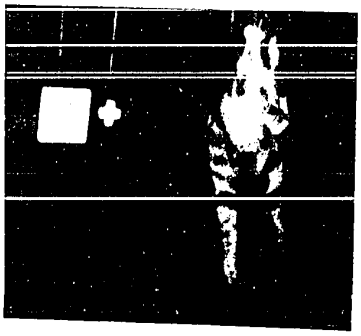


Fig.13 CAT #XXVII Normal
Stimulation: 5000:0.1 3.0v.
Feb.26 '60
Notice marked petering out of the movement within ½ second.

CAT #XXVI

Weight: 7½ lbs.

Electrode implantation: Feb. 8, '60.

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 18 mm.

Stimulations of the "normal" cat: Feb. 10, 11, 13.

Postbrachial section: Feb. 15, level of Th.4.

Stimulations after the section: Feb. 16, 17.

Cinematographic records: Feb. 10, 11, 13, 16, 17.

Site of electrode: The exposed tip of the electrode is situated ventral to the rostral pole of the inferior colliculus at the level of the oral pole of n.IV. It is well within the depth of the nucleus cuneiformis, (Fig. 18), and enters the nucleus subcuneiformis.

RESULTS

1. The "normal" cat.

A - Forelimbs

At 500:1 on Feb. 10, the fully developed movement appeared at 2.0v. (the maximum voltage used) in the form of IF f12(e34) and CF f12e34 with abduction. The threshold value for the forelimbs was 1.5v. and yielded IF f2. On Feb.

11 and 13, the complete movement, appeared quite violently at the threshold value of 1.0v. This was the maximum voltage used. The same remark applies to CF f12e34 as was made for cat no. XXIII.

The movement was in the form of a jerk: there were no latencies, the maximal development of the movement and its return to the original position usually occurred within one to two seconds. (Chart #VI, c).

At 50:5, on Feb. 10, the fully developed movement appeared at 4.0v. in the form of IF f12e34 and CF e1234 with abduction. (Fig. 15). In the former, the flexed elbow began to reverse towards extension after a few seconds latency, resulting in a marked extension-flexion tremor of this joint. There were no changes thereafter with voltage increases up to 6.5v. The threshold was 3.0v. and yielded IF f2 and CF e2 with abduction. On Feb. 11, the fully developed movement appeared at the threshold value of 2.5v. The maximum voltage used was 3.5v. On Feb. 13, the fully developed movement appeared at 3.0v. The threshold at 2.5v. yielded IF f2 and CF e2 with abduction. The maximum voltage used was 4.0v.

At this frequency there was a two seconds latency in IF and a four seconds latency in CF at threshold. The former disappeared with an increase of 0.5v., but the latter only at 2.0v. above threshold. It took 8 seconds for the movements to arrive at their maximal development at threshold

values. This time was shortened with increasing voltage until it was within one second at 2.0 - 2.5v. above threshold. The movements were not held at their maximal development till the end of the stimulation but began to peter out at about 18 seconds at threshold, this time being diminished to 15-16 seconds at 2.0 - 3.0v. above threshold. Both limbs fell to normal within one second after cessation of stimulus.

B - Head movements

On the three days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned ipsilaterally at both frequencies. The thresholds were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at thresholds higher than those of the forelimbs.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - The tail went up and to the right.

iv - The body curved with the concavity ipsilaterally.

v - Urination was often recorded during the stimulation.

vi - Shivering or coarse tremors were not observed.

vii - There were no moanings during the stimulations.

2. After the cord section.

A - Forelimbs

At 500:1, on Feb. 16, the most complete movement obtained, appeared at 4.5v. in the form of IF f12e34 and CF f2 followed after 5 to 8 seconds by e2. The threshold was 3.0v. and yielded IF f2 and CF e2 with abduction. The same movements were present on the 17th except that the thresholds were lowered by 0.5 to 1.0v. and that the fully developed movement, at 4.0v. in CF, gave f2 followed by a more fully developed e1234.

There were no latencies. The maximal development was reached within one second. This was maintained for 12 to 14 seconds, coming back to normal before the end of the stimulation at threshold values (chart #VI, c). 1.0v. above threshold, the limb fell to normal only after cessation of stimulus.

At 50:5, on Feb. 16, the most complete movement obtained, appeared at 4.5v. in the form of IF f12e34 and CF e2. The flexion of the elbow was compounded into extension after a few seconds latency in the form of a coarse tremor. CF was also compounded, e2 being preceded for a few seconds by f2 (Fig. 16 and 17). The threshold was 3.5v. and yielded IF f12e34. The maximum voltage used was 5.0v. On the 17th, the same movements were observed but at voltages 0.5v. lower. At 4.0v. CF f2 was followed by a more fully developed e1234.

A latency of 2 seconds was present at threshold for CF. The maximal development of the movements occurred at 10 seconds but this time was increased to 20 seconds at 2.0v.

above threshold. It was well maintained for the full time of stimulation. The limbs fell back to normal within 1 second after cessation of the stimulus.

B - Head movements

The head turned to the contralateral side of the stimulation on both days and at both frequencies.

C - Other movements

All disappeared except the tongue movement.

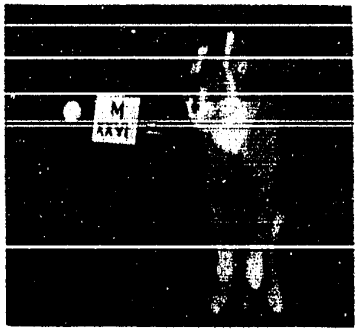



Fig.14 CAT #XXVI Lesion
Original position
Feb.16 '60

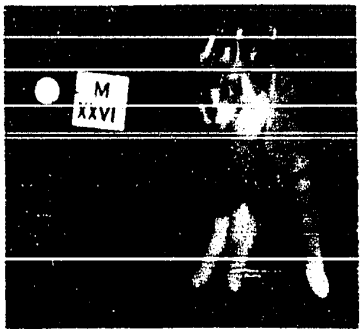



Fig.15 CAT #XXVI Normal
Stimulation: 50:5 3.5v.
Feb.10 '60
Extension of all joints and abduction of the contralateral forelimb. Elevation of the paw of the ipsilateral forelimb consequent to flexion of the shoulder and elbow. Maximal position at 5 seconds.

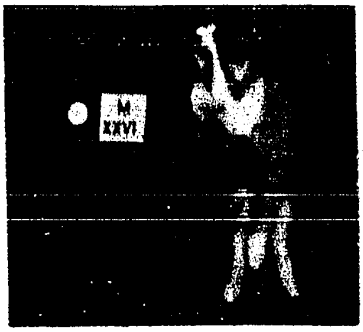



Fig.16 CAT #XXVI Lesion
Stimulation: 50:5 7.0v.
Feb.16 '60
Notice flexion of the elbow of the contralateral forelimb as the first component of a compound movement; unchanged ipsilateral forelimb.


Fig.17 CAT #XXVI Lesion
Stimulation: 50:5 7.0v.
Feb.16 '60
Notice extension of the elbow of the contralateral forelimb as the second component of the compound movement (at 19 seconds).

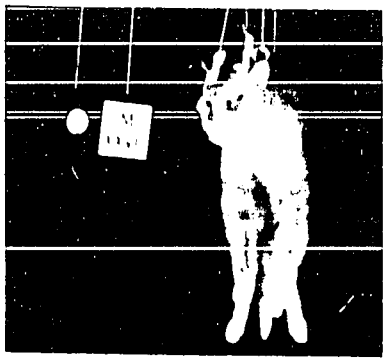


Fig.14 CAT #XXVI Lesion
Original position
Feb.16 '60

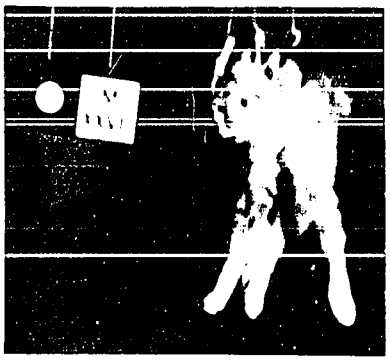


Fig.15 CAT #XXVI Normal
Stimulation: 50:5 3.5v.
Feb.10 '60
Extension of all joints and abduction of the contralateral forelimb. Elevation of the paw of the ipsilateral forelimb consequent to flexion of the shoulder and elbow. Maximal position at 5 seconds.

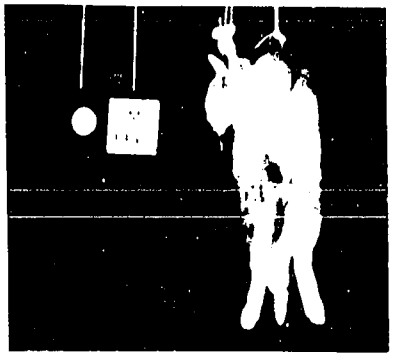


Fig.16 CAT #XXVI Lesion
Stimulation: 50:5 7.0v.
Feb.16 '60
Notice flexion of the elbow of the contralateral forelimb as the first component of a compound movement; unchanged ipsilateral forelimb.

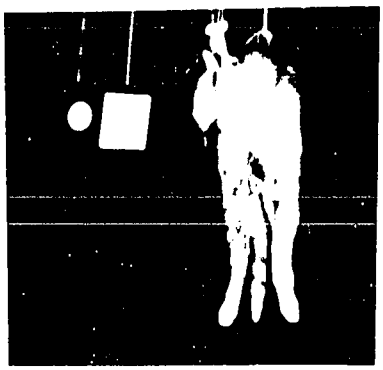


Fig.17 CAT #XXVI Lesion
Stimulation: 50:5 7.0v.
Feb.16 '60
Notice extension of the elbow of the contralateral forelimb as the second component of the compound movement (at 19 seconds).

Fig.18 Site of electrode in midbrain of CAT #XXVI

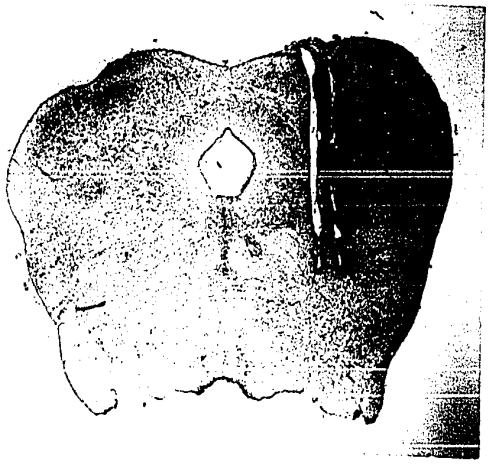


Fig.18 Site of electrode in midbrain of

CAT #XXVI

CAT #XXV

Weight: 7 lbs.

Electrode implantation: Jan. 24, '60.

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 18 mm.

Stimulations of the "normal" cat: Jan. 27, 28, 29.

Postbrachial section: Feb. 1 Level of Th.4.

Stimulations after the lesion: Feb. 2, 3, 4.

Cinematographic records: Jan. 28 and Feb. 2.

Site of the electrode: The exposed tip of the electrode was situated mainly within the nucleus cuneiformis at the level of the caudal pole of n.III. It encroaches slightly upon the very end of the rostral pole of the inferior colliculus laterally and upon the central gray medially.

RESULTS

1. The "normal" cat.

A - Forelimbs

At 500:1, on Jan. 28, the fully developed movement appeared at 2.5v. (the maximum voltage used), in the form of IF f12e34 and CF f1e234 with abduction. (Fig. 20). The

threshold was 2.0v. and yielded IF f2 and CF f1e234 with abduction. The same obtained on Jan. 29, but at values 0.5v. higher. The maximum voltage used was 3.5v.

There were no latencies. The maximal development occurred within 1 second and began to peter out after 4 to 6 seconds. The limb was back to normal before the end of the stimulation (15 sec.) at threshold, but 0.5v. above, it fell back to normal only after cessation of the stimulus.

At 50:5, on Jan. 27, the fully developed movement appeared at 4.5v. in the form of IF f12e34 and CF e1234. The threshold was 3.0v. and yielded CF abduction. The maximum voltage used was 6.0v. On Jan. 28, the fully developed movement appeared at 3.0v. (the maximum voltage used), the threshold at 2.5v. yielding IF f2 and CF e1234. The same obtained on Jan. 30, but with voltage increases up to 3.5v.

There were latencies of 4 seconds in both IF and CF at threshold. This rapidly disappeared in IF at 1.0v. above threshold, but persisted although diminished in the CF till 3.0v. above threshold. The maximal development was reached at 8 seconds at threshold. This time decreased with increasing voltage and was down to 4 seconds at 1.5 to 2.5v. above threshold. The movements were well maintained for the full time of stimulation and fell to normal within 1 second after cessation of stimulus.

B - Head movements

On the three days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned contralaterally. On the first day only, the movement was sometimes preceded by an ipsilateral turn which finally returned to the contralateral side before the end of the stimulation, at 50:5. This was never seen at 500:1.The thresholds were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at thresholds higher than those of the forelimbs.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of stimulus.

iii - The tail went up and to the right.

iv - The body curved with the concavity ipsilaterally.

v - Urination was not observed.

vi - Shivering or coarse tremors were not observed.

vii - Moanings were present during all stimulations even when a rather larger amount of anaesthetic than usual was given.

2. After the cord section.

A - Forelimbs

At 500:1, on Feb. 2, the fully developed movement appeared at 3.0v. in the form of IF f12e34 and CF f1e234 with abduction. The threshold was 2.5v. and yielded CF e2 with abduction. At 3.5v. IF was compounded by a swinging abduction preceding the original movement (Fig. 21, 22). CF was also compounded f1e234 with abduction being followed by e1f2e34 without abduction (Fig. 21, 22). On Feb. 3, the movement was fully developed at 1.5v., the compound movement appearing at 3.5v. On Feb. 4, approximately the same values obtained.

There were no latencies. The maximal development was reached within 1 to 2 seconds and began to peter out at 3 seconds at threshold, increasing to 6 seconds at 2.5v. above threshold. The limb was down to normal at 8 seconds at threshold but fell to normal only after cessation of stimulus at higher voltages. (within one second).

At 50:5, on Feb. 2, the fully developed movement appeared at 3.0v. in the form of IF f12e34 and CF e1234 with abduction. The threshold was 2.5v. and yielded CFe2. The maximum voltage used was 4.0v. On Feb. 3, the fully developed movement appeared at 3.0v. and the threshold at 2.5v. yielded IF f12 and CF e12.

Latencies of one to two seconds were present in both forelimbs at threshold. The maximal development occurred at 6 to 7 seconds in both limbs at threshold, diminishing to 3 to

5 seconds at 2.0v. above threshold. The position was maintained for the full time of stimulation and fell to normal within one second after cessation of the stimulus.

B - Head movements

The head turned contralaterally on the three days at both frequencies, although a few ipsilateral turns were recorded at 50:5 on Feb. 3.

C - Other movements

All disappeared except the tongue movements.

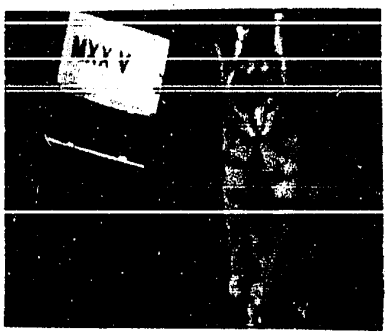


Fig.19 CAT #XXV Lesion
Original position
Feb.1 '60.

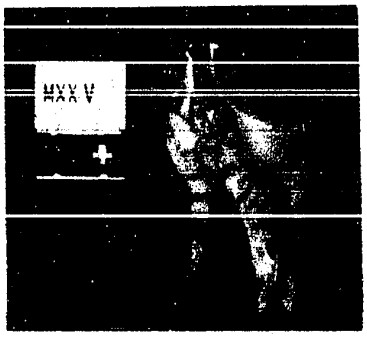


Fig.20 CAT #XXV Normal
Stimulation: 500:1 2.0v.
Jan.26 '60
Flexion of the shoulder and extension of the elbow, wrist and toes of the contralateral limb, with abduction.
Flexion of the shoulder and elbow and extension of the wrist and toes of the ipsilateral forelimb.
Maximal development within 1 second.

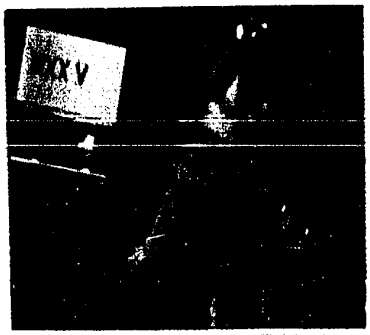


Fig.21 CAT #XXV Lesion
Stimulation: 500:1 3.5v.
Feb.1 '60
Notice the wide abduction of both forelimbs as the 1st component of a compound movement- within ½ second of onset of stimulus.

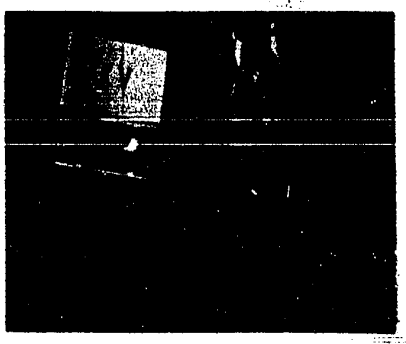


Fig.22 CAT #XXV Lesion
Stimulation: 500:1 3.5v.
Feb.1 '60
Notice that the forelimbs are back to a more medial position as the 2nd component of the compound movement- within 1½ second of onset of stimulus.

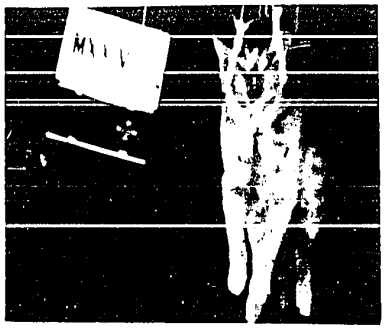


Fig.19 CAT #XXV Lesion
Original position
Feb.1 '60.

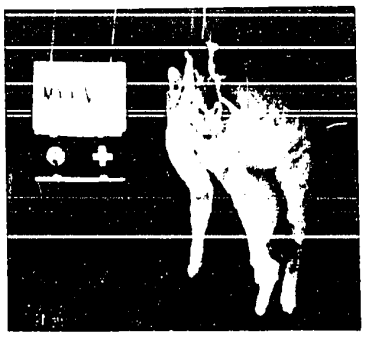


Fig.20 CAT #XXV Normal
Stimulation: 500:1 2.0v.
Jan.26 '60
Flexion of the shoulder and extension of the elbow, wrist and toes of the contralateral limb, with abduction.
Flexion of the shoulder and elbow and extension of the wrist and toes of the ipsilateral forelimb.
Maximal development within 1 second.

Fig.21 CAT #XXV Lesion
Stimulation: 500:1 3.5v.
Feb.1 '60
Notice the wide abduction of both forelimbs as the 1st component of a compound movement- within ½ second of onset of stimulus.


Fig.22 CAT #XXV Lesion
Stimulation: 500:1 3.5v.
Feb.1 '60
Notice that the forelimbs are back to a more medial position as the 2nd component of the compound movement- within 1½ second of onset of stimulus.

CAT #XXIV

Weight 7½ lbs.

Electrode implantation: Dec. 28, '59.

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 18 mm.

Stimulations of the "normal" cat: Dec. 29, 30, '59
Jan. 4, 5, '60.

Postbrachial section: Jan. 5. Level of Th.4.

Stimulations after the lesion: Jan. 6, 7, '60.

Cinematographic records: Dec. 29, 30. Jan. 5, 6, 7.

Site of electrode: The electrode is dorsolateral to the central gray within the rostral pole of the nucleus of the inferior colliculus where the intercollicular fibers suddenly fan out in and around the nucleus. It encroaches slightly upon the central gray.

RESULTS

1. The "normal" cat.

A - Forelimbs

No movements were ever obtained from this cat at 500:1 (up to 10v.).

At 50:5 on Dec. 29, the only movements obtained were a rythmic adduction of both forelimbs q. 2 seconds. On Dec.

30, the most complete movement obtained, appeared at 6.5v. in the form of IF fl2 with adduction and CF fl2 with adduction. The threshold was 5.0v. and yielded only an ill-defined rythmic adduction of both forelimb q. 2 seconds. The maximum voltage used was 7.5v. On Jan. 4, the most complete movement obtained appeared at 8.0v. and the threshold was at 6.5v. On Jan. 5, the most complete movement was at 8.5v. and the threshold, at 7.5v. The maximum voltage used was IIv.

Long latencies of 10 seconds were present at threshold in both forelimbs. This was shortened progressively to 5 seconds at 2.0v. above threshold. The time for the maximal development of the movement was 15 seconds at threshold, diminishing progressively to 10 seconds at 2.0v. above threshold. These were well maintained for the full time of stimulation and fell back to their original position within one second after cessation of the stimulus.

B - Head movements

On the four days of stimulation, the pupils dilated, the eyelids retracted, and the head was dorsiflexed symmetrically. The thresholds were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at lower voltages than the forelimbs in the form of elf2.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - The tail did not curve.

iv - The body did not curve.

v - Urination was not observed.

vi - Shivering or coarse tremors were not observed.

vii - There were no moanings during the stimulations.

2. After the cord section.

A - Forelimbs

At 500:1, no movements could be obtained after the lesion.

At 50:5, on Jan. 6, no movements could be obtained until 10v. when a rythmic adduction of the forelimbs appeared, of very minimal intensity. On Jan. 7, no movement could be obtained until 32v. when the same rythmic adduction of the forelimbs appeared. At 34v., the head turned to the contralateral side and the CF yielded e2 with abduction. If the stimulations were continued at 2 minutes interval, this movement would disappear completely, and rest periods of over 15 minutes had to be given between each stimulation for the movement to be kept at the same intensity.

Time relationships were not determined in this cat.

B - Head movements

No movements were obtained at 500:1. At 50:5, the pupils dilated, the eyelids and nictitating membranes retracted and the head turned contralaterally on Jan. 7.

C - Other movements

All disappeared except the tongue movements.

CAT #XIX

Weight: 7½ lbs.

Electrode implantation: Oct. 13, '59.

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 19 mm.

Stimulations of the "normal" cat: Oct. 14, 15, 16.

Postbrachial section: Oct. 18. Level of Th.3.

Stimulations after the cord section: Oct. 19, 20.

Cinematographic records: Oct. 15, 16, 19.

Site of electrode: The exposed tip of the electrode is situated ventral to the rostral pole of the inferior colliculus at the level of the oral pole of n.IV. It is well within the depth of the nucleus cuneiformis (see cat #XXVI, Fig. 18). The very end of the tip touches the nucleus subcuneiformis.

RESULTS

1. The "normal" cat.

A - Forelimbs

At 500:1, no movements appeared on Oct. 14. On Oct. 15, the most complete movement obtained was f12 from the threshold value 2.5v. to the maximum voltage used of 4.0v.

No CF movements were obtained. (Fig. 25).

There were no latencies. The maximal development was obtained within 1 second after the onset of stimulation. It began to peter out at 5 seconds. The limbs fell to their original position after 10 seconds at threshold and 0,5v. above that value. This occurred only after cessation of the stimulus at 1.0 - 1.5v. above threshold. (Chart #VI, b). The same movements and time relationships obtained on Oct. 16.

At 50:5, on Oct. 14, no movements were obtained. On Oct. 15, the most complete movement obtained, appeared at the threshold value of 2.5v. in the form of IF e1234 and CF e2 with abduction (Fig. 24). The same obtained until the maximum voltage used, i.e., 4.0v. On Oct. 16, IF e1234 appeared at the threshold value of 3.0v., and CF e2 with abduction at 3.5v. At 5.0v., IF was compounded, IF f2 preceding the usual e1234 for a period of 5 seconds.

Latencies in CF were of the order of 8 seconds at threshold diminishing to 5 seconds at 2.0v. above. The maximal development was reached at 13 seconds at threshold, quickening to 10 seconds above that value. There were no latencies in IF. The maximal development was reached in both at 8 seconds at threshold. This diminished to 3 seconds at 1.5v. above threshold. With the appearance of the compound movement however, this time was lengthened to 15 seconds at 2.5v. above threshold.

In both limbs the maximal position was well maintained for the full time of stimulation. They fell back to the original position within 1 second (occasionally 3 or 5 seconds) after the end of the stimulation.

B - Head movements

On the three successive days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted, and the head turned ipsilaterally at both frequencies. Poststimulatory reversals were present on the first day only at 50:5. The thresholds were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at threshold higher than those of the forelimb.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of the stimulus.

iii - Tail movements were not observed.

iv - The body did not curve.

v - Urination was not observed.

vi - Shivering or coarse tremors were not observed.

vii - There were no moanings during the stimulations.

2. After the cord lesion.

A - Forelimbs

At 500:1, on Oct. 19, the most complete movement obtained appeared at 4.0v. in the form of IF f12. No change

occurred until the maximum voltage used, i.e., 6.0v. The same obtained on Oct. 20.

There were no latencies. The time for the maximal development was 3 seconds at threshold but occurred within 1 second at 1.0v. above this value. This position was held for 8 seconds at threshold, increasing to 18 seconds at 2.0v. above threshold. The limb was back to normal at 15 seconds at threshold but this time was prolonged with increasing voltage so that it fell back to its original position 10 seconds after cessation of the stimulus at 1.5v. above threshold. (Chart #VI, b).

At 50:5, on Oct. 19, the most complete movement obtained appeared at 5.0v. in the form of IF f12 and CF f12 (Fig. 26). CF was a bit more flexed at the elbow and IF, a bit more at the shoulder bringing the paw of CF in front of that of IF. The threshold was 4.5v. and yielded CF f12. The maximum voltage used was 6.0v. On Oct. 20, the same obtained for IF but CF movements disappeared completely.

No latencies were present in either limbs. The time for the maximal development in CF was 15 seconds at all voltages. The position was held for the full time of stimulation and fell to normal 5 seconds after cessation of the stimulus. The time for the maximal development in IF was 10 seconds at threshold but was down to 4 seconds at 1.0 - 1.5v. above threshold. This position was well maintained for the full time of stimulation and fell to normal within 1 second after cessation of the stimulus. (5

seconds at threshold).

B - Head movements

On the two days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned ipsilaterally at both frequencies.

C - Other movements

All disappeared except the tongue movements.

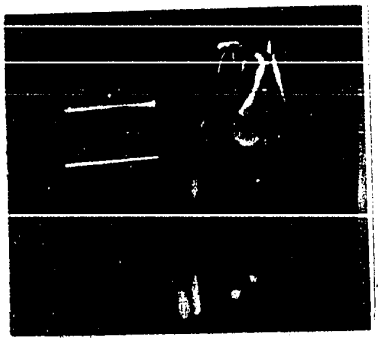


Fig.23 CAT #XIX Normal
Original position
Oct.16 '59

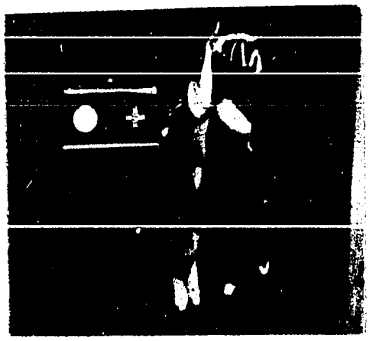


Fig.24 CAT #XIX Normal
Stimulation: 50:5 3.2v.
Oct.16 '59
Notice extension of the elbow and abduction of the contralateral forelimb; extension of the shoulder and elbow of the ipsilateral forelimb.
Maximal development at 15 seconds.

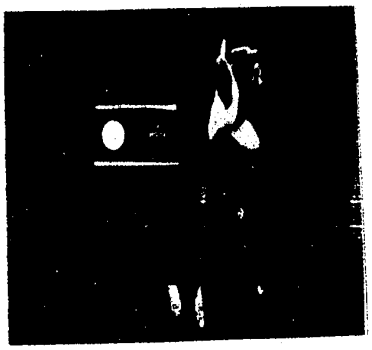


Fig.25 CAT #XIX Normal
Stimulation: 500:1 2.6v.
Oct.16 '59
Flexion of the shoulder and elbow of the ipsilateral forelimb. Absence of movement in the contralateral forelimb.
Maximal development within 1 second.

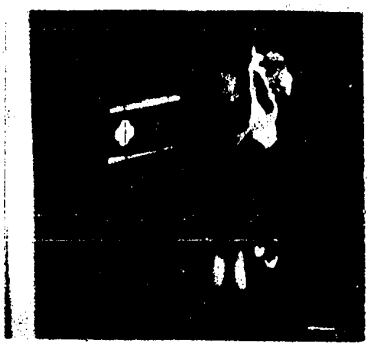


Fig.26 CAT #XIX Lesion
Stimulation: 50:5 5.5v.
Oct.19 '59
Notice flexion of both elbows after the lesion.
Maximal development at 15 seconds.

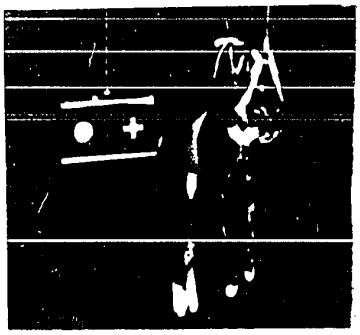


Fig.23 CAT #XIX Normal
Original position
Oct.16 '59

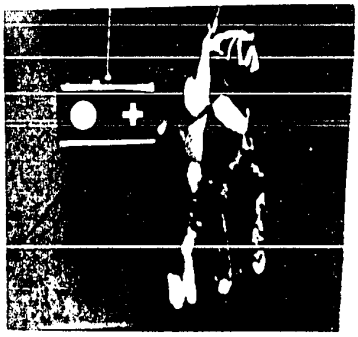


Fig.24 CAT #XIX Normal
Stimulation: 50:5 3.2v.
Oct.16 '59
Notice extension of the elbow and abduction of the contralateral forelimb; extension of the shoulder and elbow of the ipsilateral forelimb.
Maximal development at 15 seconds.

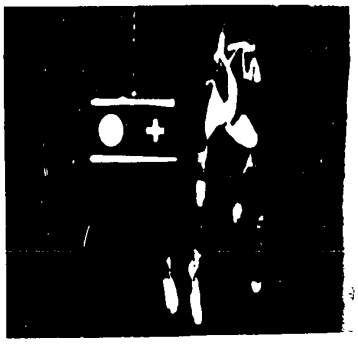


Fig.25 CAT #XIX Normal
Stimulation: 500:1 2.8v.
Oct.16 '59
Flexion of the shoulder and elbow of the ipsilateral forelimb. Absence of movement in the contralateral forelimb.
Maximal development within 1 second.

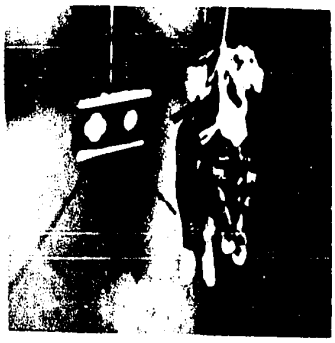


Fig.26 CAT #XIX Lesion
Stimulation: 50:5 5.5v.
Oct.19 '59
Notice flexion of both elbows after the lesion.
Maximal development at 15 seconds.

CAT #XVIII

Weight: 8.0 lbs.

Electrode implantation: Sept. 28, '59.

Stereotaxic coordinates: Frontal plane 0, 2.5 mm. to the right of the midline.

Depth of electrode: 19 mm.

Stimulation of the "normal" cat: Sept. 29, Oct. 1, 2.

Postbrachial section: Oct. 6. Level of Th. 3.

Stimulations after the cord section: Oct. 7.

Cinematographic records: Sept. 29, Oct. 7.

Site of electrode: Not determined histologically.

## RESULTS

1. The "normal" cat.

A - Forelimbs

At 500:1, on Sept. 29, the most complete movement obtained appeared at the threshold value of 6.0v. in the form of CF fle2 with abduction. This was the maximum voltage used. On Oct. 1, CF fle2 appeared at 3.5v. and IF fle2 appeared at 5.0v. (the maximum voltage used). The same obtained on Oct. 2.

The time relationships were not determined in detail. Grossly, they consisted of a quick development to the maximal position which is not maintained for the full time of stimulation, and falls to normal immediately after cessation of the stimulus.

At 50:5, on Sept. 29, the same movements obtained, CF appearing at 6.0v. and IF at 6.5v. (the maximum voltage used). On Oct. 1, CF and IF appeared at 5.0v. The maximum voltage used was 6.0v.

There were no latencies. The maximal position was slow to develop and was well maintained for the full time of stimulation. The time for the limb to fall to its original position was not determined.

B - Head movements

On the three successive days of stimulation, the pupils dilated, the eyelids and the nictitating membranes retracted and the head turned contralaterally. Occasional poststimulatory reversals were recorded on the first two days of stimulation at 50:5 only. The thresholds were lower than those of the forelimbs.

C - Other movements

i - Hindlimb movements appeared at thresholds higher than those of the forelimb.

ii - The tongue protruded continually during the stimulation session and there were usually licking movements immediately after cessation of stimulus.

iii - The tail went up and to the right.

iv - The body curved with the concavity ipsilaterally.

v - Urination was occasionally recorded.

vi - Shivering or coarse tremors were not observed.

vii - There were no moanings present during the stimulations.

2. After the cord section.

A - Forelimbs

At 500:1, the movement was very small and could not be analysed in terms of joints. The most completely developed movement available appeared at 4.0v. and gave a slight backward movement of CF paw, with a similarly slight foreward movement of IF. At 5.0v. this movement was compounded so that a reversal of this appeared after a long latency (circa 12-15 seconds) CF slipping forewards and IF backwards.

There were no latencies. The maximal development occurred within one second of the onset of stimulus. The reversal occurred at about 12-15 seconds. The limbs fell back to their original position within one second after cessation of stimulus.

At 50:5, the most complete movement occurred at 4.0v. (the threshold value), in the form of CF fle2 and IF fl2. The maximum voltage used was 7.0v.

There were no latencies. The movement took a relatively long time to develop, was held for the full time of stimulus, and took a comparatively long time to come back to normal (8 seconds).

B - Head movements

The pupils dilated, the eyelids and the nictitating membranes retracted and the head turned contralaterally at both frequencies.

C - Other movements

All disappeared except the tongue movements.

SPECIAL SERIES OF STIMULATIONS
performed on the "normal" cat
#XXVII on February 26.

This series of stimulations was done to study the progression of the time relationships over a wide range of frequencies.

Exact thresholds for the barest dilatation of the pupils, at 0.2v. intervals were determined at frequencies of 10, 25, 50, 100, 250, 500, 750, 1000, 1500, 2000, 3000, 4000, and 5000 cps with a constant impulse duration of 0.1 msec. The results were as given in Chart #1. Note that the threshold decreases abruptly from 10 to 250, levels off to be at its lowest at 500 and 750 cps and then slightly increases again to be constant from 1500 to 5000 cps.

The cat was then stimulated with the same parameters but 2.0v. above this pupillary threshold to obtain good forelimb movements. The time relationships were observed at all these parameters and the results tabulated in Chart #2.

There were no latencies at any frequency. The time for the maximal development decreased abruptly from 10 seconds at 50 and 100 cps to one second at 500 cps. The time for the maintenance of this maximal position decreased from the full time of stimulation at 50 and 100 cps to 5 seconds at 500, and finally to one second at 3000 cps. At the latter frequency therefore we have a quick movement which goes up to a maximum

and starts immediately to peter out as this position is reached. (See cat #XXVII, fig. 12, 13 - p.44). The time for the limbs to be back to their original position diminishes from 5 seconds after cessation of the stimulus at 50 and 100 cps, to 10 seconds after the onset of stimulation at 750 and 1000 cps, to 6 seconds at 3000 and finally to 2 seconds at 5000 cps. At the latter frequency, therefore, the movement is nothing but a rapid jerk immediately back to the original position.

Leaves 72 and 73 repeated in page numbering.

# CHAPTER IV

## COMPILATION OF RESULTS

### I - Nature of the movements

1. In the "normal" cat.

A - Patterns of Movements (Chart #IV).

Forty different movements could be elicited from the forelimbs (2 forelimbs in 10 cats at 2 frequencies), 3 of which were actually an absence of movement, i.e., XXIV in both forelimbs at 500:1 and XIX in the contralateral forelimb at the same frequency.

Flexion of the shoulder and elbow, extension of the wrist and toes with abduction (f12e34, abd) were obtained three times in the contralateral limb, (cat #XXIII at both frequencies and #XXVI at 500:1) and ten times without abduction in the ipsilateral forelimb, (cats # XXVI, XXV, XXIII, XXII, XXI at both frequencies). Flexion of the shoulder and elbow alone, (f12) occurred once in the contralateral limb, (XXIV at 50:5) and six times in the ipsilateral limb, (XXVII and XX at both frequencies, XXIV at 50:5, XIX at 500:1). Presumably this is the same basic movement as f12e34 since movement at the wrist and toes was always extension when the effect of the stimulation finally spread to the muscles controlling these joints.

Flexion of the shoulder and extension of the elbow, wrist and toes with abduction (f1e234, abd.) occurred seven times in the contralateral, (XXVII, XXII, XXI at both fre-

quencies and XXV at 500:1) and once in the ipsilateral forelimb (XXVI at 50:5); the latter was the second component of a compound movement. Flexion of the shoulder and extension of the elbow alone (fle2) occurred four times (in both limbs at both frequencies in cat #XVIII).

Extension of all joints with abduction occurred twice in the contralateral forelimb in cats #XXVI and XXV at 50:5, and once without abduction in the ipsilateral forelimb of cat #XIX also at 50:5. The extension of the shoulder and elbow alone as recorded in the contralateral forelimb of cat #XX at both frequencies is probably the same movement.

For the IPSILATERAL forelimb therefore, if IF f12 is assimilated to f12e34, it can be said that this pattern was obtained 16 times, i.e., in 7 cats at both frequencies (XXVII, XXVI, XXV, XXIII, XXII, XXI, XX) and in two others at one frequency only: at 50:5 in cat #XXIV in which movements were absent at 500:1, and at 500:1 in #XIX. Exceptions to this movement were obtained only three times; at both frequencies in cat #XVIII giving flexion of the shoulder and extension of the elbow, and at 50:5 in #XIX giving extension of all joints.

For the CONTRALATERAL forelimb, if fle2 is assimilated to fle234 and el2 to el234, it can be said that extension of the elbow, wrist and toes were observed 13 times, i.e., at both frequencies in 6 cats (XXVII, XXV, XXII, XXI, XX, XVIII) and at 50:5 only in cat #XIX. This movement was accom-

panied 9 times by flexion of the shoulder, i.e., at both frequencies in 4 cats (XXVII, XXII, XXI, XVIII) and at 500:1 in cat #XXV. It was accompanied by extension of the shoulder 4 times, i.e., at both frequencies in cat #XX and at 50:5 only in cats #XXVI and XXV. Only 4 times did the contralateral forelimb not give extension of the elbow. It yielded flexion of the shoulder and elbow at 50:5 in cat #XXIV, at both frequencies in cat #XXIII and at 500:1 in cat #XXVI. The latter two however gave a response very much like the usual contralateral movement, the limb being abducted and the elbow being hardly flexed.

The movements obtained in the forelimbs in this series of experiments clearly show that one cannot speak of flexion or extension of a limb as done by previous investigators. This indeed implies that all joints flex or extend together. One must therefore distinguish between patterns in which all joints perform the same movement and those in which they do not. As already mentioned in the introduction, the former are referred to as "simple" movements, the latter, as "composite" patterns. These are further qualified by the terms complete or imcomplete depending on whether all the joints of the limb were involved or not. Another type of movement is one in which a reversal occurs in at least one of the joints during the stimulation. This reversal never occurs at threshold value and is rarely seen at voltages just sufficient to evoke a fully

developed movement. When it is present, it is usually found at still higher voltages. The second component added when the movement is compounded may precede or follow the original one, i.e., a joint which gave flexion may with increasing voltage extend before flexing or extend after the original flexion. This type of movement is the one referred to as a compound movement.

The majority of movements were composite.

Only three simple complete movements were observed and all three, at 50:5. They consisted in extension of all joints in the contralateral forelimbs of cats #XXVI and XXV, and in the ipsilateral forelimb of cat #XIX. CF el2 found at both frequencies in cat #XI might be added to these 3 as being part of a simple movement but since e34 did not appear with voltage increases up to 15v., they are not included with the group. No simple movement with flexion of all joints was ever recorded.

Two compound movements have been noted in the forelimbs of the normal cat. The first was in the ipsilateral forelimb of cat #XXVI at 50:5, in which the originally flexed elbow is followed by extension. The second was in the ipsilateral forelimb of cat #XIX at 50:5, in which the originally extended shoulder, elbow, wrist and toes are preceded by a flexion of the elbow after increasing the voltage. (One of the nicest compound movements seen, was in the ipsilateral

hindlimb of cat #XXI where f1234 shifts back to fle234, the original low voltage movement, during the time of stimulation.)

That no simple movements with flexion of all joints was ever recorded in the forelimbs is immediately obvious when the movements are grouped by joints (Chart #III). Indeed wrists and toes have given extension at all times when an active movement was observed. The only flexions observed at the wrists were passive ones due to gravity when the stimulus was only strong enough to involve the shoulder and elbow. If these are flexed, the forearm moves towards the horizontal position, and the paw droops slightly downwards. These were not recorded. A slight increase in voltage usually counteracts the gravitational force and the wrist extends forcibly as the toes fan out in extension.

The shoulder in the contralateral forelimb at 500:1 has given flexion seven times and extension only once and this in cat #XI in which the electrode position was displaced quite far laterally. At 50:5, however, the same joint has given extension three times, i.e., in cats #XXVI, XXV, and XI; flexion was obtained six times. It should be noted that it was only in the first two of these cats that a simple complete movement was observed in this forelimb. There seems to be a greater propensity for extension in this joint at the lower frequency.

In the ipsilateral forelimb at 500:1, the shoulder flexed in nine cats, one of which extended at low voltage, i.e., cat #XXI. At 50:5 all shoulders were flexed except in cat #XIX where it was extended.

The elbow in the contralateral forelimb at 500:1 extended six times and flexed twice. One of these flexed elbows (cat #XXVI) extended at 50:5. Moreover in cat #XIX, the contralateral forelimb which was motionless at 500:1 gave an extended elbow at 50:5. (Note that there is also a flexion of the elbow at 50:5 with a motionless contralateral forelimb at 500:1, but cat #XXIV in which this occurred has its electrode implanted in the inferior colliculus). There is again here a greater tendency for extension at 50:5.

The elbow in the ipsilateral forelimb at 500:1 was flexed in all cats except #XVIII where it was extended. At 50:5 the same held true except that extension was also found in the elbow of cat #XIX and in that of cat #XXVI at least as the second component of an abortive compound movement.

B - Changes in the nature of the movement with changes in frequency.

In all, 5 cats showed a change in movement in at least one of its limbs with a change in frequency, i.e., #XXVI, XXV, XXIV, XXI, XIX. The five others, XXVII, XXIII, XXII, XX, and XVIII showed no change with frequency.

Changes were found in the contralateral forelimb of four animals, i.e., #XXVII, XXV, XXIV, and XIX. Cats #XXIV and XIX showed only an absence of movement at 500:1, but XXVI and XXV showed an actual reversal of the movement. In XXVI, the flexion of the shoulder and elbow at 500:1 changed to extension of the same two joints at 50:5. In XXV the flexed shoulder at 500:1 became extended at 50:5. There were no changes in the other six cats in this limb.

Similar changes have been observed in the ipsilateral forelimb of 4 cats, i.e., XXVI, XXIV, XXI, XIX. Again XXIV showed only an absence of movement, at 500:1. In cat #XXVI, the flexion of the elbow acquired an extensor component after a latency at 50:5 but was purely flexor at 500:1. #XXI extended its shoulder at low voltage at 500:1 but was always flexed at 50:5. #XIX, with flexed shoulder and elbow at 500:1, extends both (and the wrist and toes) at 50:5. There seems again to be (except for the shoulder of #XXI) a favoring of extension at 50:5 in the shoulder and elbow of both limbs.

C - Thresholds and order of appearance of movements.

The head movements had the lowest thresholds in all cats. With increasing voltage, the forelimb movements then appeared followed by the hindlimbs. This also obtained in all cats except #XXIV in which the hindlimb movements preceded those of the forelimb, and in cat #XXI in which the ipsilateral hindlimb appeared before the contralateral forelimb.

The ipsilateral and contralateral forelimb movements have similar thresholds, both appearing together, or one or the other appearing first on different days.

The thresholds for the appearance of the forelimb movements was of the order of 2.0 - 2.5v. at 500:1 in all cats except #XX, and XVIII (10.0 and 4.0v. respectively). At 50:5, the thresholds were 2.5 - 3.0v. in all except #XXIV, XX and XVIII (11.0 - 6.0 - 5.5v. respectively). It should be noted that cats #XXIV and XX do not have their electrodes implanted within the nucleus cuneiformis; the position of the electrode of cat #XVIII was not determined histologically.

When the fully developed movement does not appear at threshold, the first joint to move in the forelimbs is the elbow followed or accompanied by the shoulders. The wrist and toes are the last to appear. This successive appearance of the various joints is completely unrelated to the position of the electrodes.

D - Conclusions

i - The movements obtained are more complex than suggested by other authors. Only 3 simple complete movements have been found in a total of 40 possible movements.

ii - The most frequent patterns observed are flexion of the shoulder and elbow with extension of the wrist and toes, in the ipsilateral forelimb; extension of the elbow, wrist and

toes, with abduction and a variable shoulder in the contralateral forelimb.

iii - The only active movements obtained from the wrist and toes in either limbs was extension.

iv - The threshold values increase from elbows to shoulders and finally to the wrist and toes.

v - Changes in the movements do occur with changes in the frequency, and they usually favor extension at the lower and flexion at the higher frequency.

2. After the postbrachial section.

A - Changes in the patterns of movements.

The six cats with lesions showed some change in the nature of the movements elicited by stimulation of the midbrain reticular formation. Of the 24 movements available, (3 of which were actually an absence of movement, i.e., at 500:1 in the contralateral forelimb of cat #XIX and in both forelimbs of cat #XXIV) only 8 were unchanged. (Chart #V).

The elbow shifted from extension to flexion in seven movements. Five were in the contralateral forelimb, i.e., at both frequencies in cat #XXVII; at 50:5 in #XXVI (as the first component of a compound movement) and XIX; and at 500:1 in #XXV (as the second component of a compound movement). The other two were in the ipsilateral forelimb, i.e., at 50:5 in cats #XIX and XVIII. A change in the elbow from flexion to extension was seen twice in the contralateral forelimb, i.e.,

at 50:5 in cat #XXIV and at 500:1 in cat #XXVI as the second component of a compound movement.

N.B. In cat #XXVI since the original movement was difficult to classify in relation to the elbow, it might just as well be said that it acquired a flexor component as the first of a compound movement.

There were five changes in the shoulder. It shifted from flexion to extension four times in the contralateral forelimbs: at both frequencies in cat #XXVII and at 500:1 in #XXV as the second component of a compound movement and in #XXVI. The fourth change was the reverse, i.e., a change from extension to flexion in the ipsilateral forelimb at 50:5 in cat #XIX.

Other changes recorded were a swinging abduction as the first component of a compound movement at 500:1 in cat #XXV and un unanalysable forewards and backwards movement as described in both limbs at 500:1 in cat #XVIII.

Of the three original simple complete patterns of movement, 2 retained their original extension of all joints, i.e., at 50:5 in cats #XXV and XXVI, although in the latter the extension of the elbow was preceded by a flexion to form a compound movement at high voltages. The extended limb in cat #XIX (which had also been preceded by flexion of the elbow in the intact cat at high voltages) became flexed at the shoulder and elbow after the lesion.

Of the two original compound movements, one, as seen above, was changed in favor of the flexor component; the other, at 50:5 in the ipsilateral forelimb of cat #XXVI remained unaltered.

Six new compounded movements appeared, 5 of which were at 500:1 where previously no compound movements had been observed. They were in the contralateral forelimb of cats #XXVI, XXV and XVIII and in the ipsilateral forelimb of #XXV and XVIII. The sixth developed at 50:5 in the ipsilateral forelimb of cat #XXVI.

In the CONTRALATERAL forelimb therefore, the elbow movements were all changed after the lesion except at 50:5 in cat #XXV and XVIII. Five changed from extension to flexion; two, from flexion to extension; one yielded the ill-defined backwards-forewards compound movement already referred to at 500:1. Two which did not respond before were just as motionless after the lesion. In the same limb, the shoulder movement was reversed four times and remained unchanged five times (notice that an absence of movement is not recorded as a change). The changes were a shift from flexion to extension four times: at 50:5 in cats #XXVII and at 500:1 in #XXVII, XXVI and XXV. The ill-defined movement described at 500:1 in cat #XVIII might be given as a 5th change.

In the IPSILATERAL forelimb the 8 normal flexions of the elbow remained unaltered and of the three extensions of the same joint, two were changed to a definite flexion: at

50:5 in cats #XIX and XVIII. The third gave the ill-defined compound movement described above for cat #XVIII at 500:1. Only one shoulder exhibited a reversed movement after the lesion in this limb. Cat #XIX changed from extension to flexion at 50:5.

B - Thresholds

The voltages at which a change in the movement were found in cats #XXVII, XXVI and XXIV were higher than the maximal voltage used in the intact preparation. In these three the thresholds for the forelimb movements had been considerably increased. The changes occured at threshold.

In cats #XXV, XIX and XVIII, though the threshold is similarly increased in the first two after the lesion, the voltage at which a change was found after the lesion, was not greater than the maximal voltage used in the "normal" animal.

C - Conclusion

i - The postbrachial section modified the patterns of movements elicited in the forelimbs by stimulation of the midbrain reticular formation.

ii - The most readily reversed movement is that of the elbow of the contralateral limb. Its position was changed in nearly every instance from extension to flexion but also to extension if the original movement was a flexion.

iii - The elbow of the ipsilateral limb was unchanged from its usually flexed position. The few extensions found in this elbow were reversed, however, after the lesion.

iv - The shoulder of the contralateral limb passed from flexion to extension in four cases, and that of the ipsilateral limb did the reverse in one instance.

v - The wrists and toes were unchanged after the lesion. When an active movement was elicited it was always extension, although sometimes no movements could be obtained.

vi - There is an increase in threshold values for eliciting patterns of movements after the lesion.

## II - Time Relationships

1. In the "normal" cat.

At 500:1, latencies were absent except occasionally at threshold value when a 1 or 2 seconds latency was recorded. The maximal development occurred within one second after the onset of stimulation, except again occasionally at threshold, when a delay of 2 to 3 seconds was observed. This maximal position was not well maintained but started to peter out from 4 to 14 seconds after the onset of stimulus (range at all voltages used in all cats). At threshold and close to threshold, the limb was completely back to its original position before the end of stimulation in about half the cats. At

higher voltages in these and at all voltages in the other cats, this obtained only after cessation of stimulus (usually within one second). Exceptions to these timings were found in cats #XX and XXIV. Cat #XX had a long four seconds latency, with a maximal development at 5 seconds. This was well maintained for the full time of stimulation and fell to normal within three seconds after cessation of stimulus. The electrode was misplaced far laterally to the periphery of the brainstem. Cat #XXIV gave no limb movements at this frequency: the electrode was implanted within the nucleus of the inferior colliculus and encroached slightly upon the central gray. A special mention must be made of cat #XXVI which showed an exaggeration of 500:1 timings. The whole movement appeared as a jerk; there were no latencies; the maximal development petered out within ½ second; the limb was back to normal within 2 seconds from the onset of stimulus. The electrode was implanted within the depth of the nucleus cuneiformis and entered the nucleus subcuneiformis.

At 50:5, latencies were nearly always present at threshold, (except in the ipsilateral forelimb of cat #XIX). This latency was usually longer in the contralateral forelimb and diminished more slowly with increasing voltage than in the ipsilateral forelimb (#XXVI, XXV, XXII, XXI, XX, XIX). The reverse was observed in cat #XX and equality of the two limbs in cats #XXVII, XXIV, XXIII, XVIII. The maximal development

appeared within 4 to 10 seconds at threshold and this time was shortened with increasing voltage. The position is well maintained for the full time of stimulation at threshold in all cats except #XXVI. Above threshold in cats #XXIII, XXII, XXI and of course #XXVI, there was a tendency for petering out sooner. The limbs fell back to their original position within one second after cessation of stimulus except in both forelimbs of cats #XXVII, XX and in the ipsilateral forelimb of # XXIII. It seems surprising that increasing voltage which reduces the latency and the time for the maximal development should reduce the time of the effect. (XXVII, XXIII (CF), XXII and XXI). At 50:5 therefore we usually have latencies, greater in the contralateral forelimb; the movements are slow and deliberate, fully maintained for the full time of stimulation and falling back to normal only after cessation of the stimulus.

These differences between the two frequencies fall within a wide range of values for the various timings under consideration, if a greater variety of frequencies is utilised. As reported above for cat #XXVII, (Chart #1), very low frequencies (10 to 20 cps) give a tremulous movement which follows the rate of stimulation. Between 20 to 30 cps the movement becomes tonic and has the same characteristics as those described under 50:5. As the frequency is increased up to 250 cps the characteristics of 500:1 begin to appear. The time for the

maximal development gradually diminishes and the position begins the peter out before the end of the stimulation. These parameters are all shortened as the frequency is increased until only a jerk is observed at 5000 cps.

2. After the lesion.

At 50:5 there were no significant changes except in cats #XIX and XXVI. In the former, the latencies were lost in the contralateral forelimb. In cat #XXVI the time for the limbs to reach their maximal development was increased from 8-1 sec. to 10-20 seconds. The voltage at which a fully developed movement could be obtained in these cats before and after the lesion were 4.0v. and 4.0v. respectively in #XXVI and 2.5 - 5.0v. respectively in #XIX.

At 500:1, there were no significant changes except in cats #XXVI and XIX. The time at which the limb was held in its maximal position was greatly prolonged in both after the lesion: from 1 to 13 seconds in #XXVI and from 5 to 8-18 seconds in #XIX (Chart #V, b & c). The time at which the limb fell back to normal was also prolonged from 2 to 21 seconds in #XXVI and less significantly from 10-21 to 15-30 seconds in #XIX. It is not believed that the changes in the timings in cat #XIX were due to the increase in the absolute voltage used, for similar changes are also found in cat #XXVI in which the voltage threshold was unchanged. Cat #XXVII on the other hand, in which the timings were unaltered, also showed a great increase

in threshold (3.0 - 6.0v.). It should be noted that the only similarity between cats #XIX and XXVI is that the electrode is better implanted within the depth of the nucleus cuneiformis.

From these changes very few generalizations can be made as to the effect of a postbrachial section upon the time relationships. It does seem justifiable, however, to say that the limb may be held better at its maximal position after the section. This has occurred in 2 out of 4 cats.

3. Conclusions

i - Different frequencies give movements having different time relationships. 500 cps yields a quick movement which cannot be maintained for the full 20 seconds of stimulation. 50 cps elicits a slow movements well maintained for 20 seconds.

ii - Postbrachial sections do not seem to change these time relationships consistently. Two cats, however, seem to indicate that the movement is better maintained at high frequencies after the lesion.

# CHAPTER V

## DISCUSSION

### 1. Nature of the movement observed in the "normal" cat.

It is apparently not sufficient to speak of flexion or extension of a limb when reporting the movements elicited by stimulation of the reticular formation of the brainstem. This indeed seems to imply that all joints in the limb flex or extend. Such simple complete movements were found only three times in this series of experiments. They consisted of extension of the shoulder, elbow, wrist and toes in the ipsilateral forelimb of cat #XIX at 50:5 and the same with abduction in the contralateral forelimb of cats #XXV and XXVI at the same frequency. No simple complete movements of flexion were recorded. Indeed no active flexion of the wrist and toes was ever observed. It should be stated, however, that passive drooping of the wrist did occur at low voltages as the flexion of the shoulder and elbow lifted the forearm to the horizontal position.

Why, then, did Thiele, (32), Hinsey et al. (8), and Sprague and Chambers (31), speak of flexion or extension of the limbs as though they were simple movements? There are two possibilities. 1) They did obtain simple movements. Sprague and Chambers introduced their electrode into the medulla oblongata and could stimulate cells and fibers of the

reticular formation with direct connections to the spinal cord. (Brodal, 2). This might give a more constant and basic pattern than stimulation of the midbrain. The obvious objection is that Ranson and Hinsey also described such simple movements by stimulation of the midbrain. The latter however performed the experiments in decerebrate preparations. Would the midbrain of a decerebrate cat yield the same pattern as the medulla of an intact animal? This is not altogether impossible since departures from this basic pattern, as obtained by stimulation of the midbrain in normal cats, could be due to circuitous pathways through higher midbrain, pretectal and diencephalic areas. Indeed, Ingram et al. did describe protrusion of the claws and fanning of the toes with flexion of the limb, in their series of stimulations of the midbrain in the normal cat. ii) A more likely interpretation, is that these authors did not feel the need for a detailed description of joint movements and referred only to the general movement of the limb. If only the elbow joint is considered, (the movement of which determines to the greatest extent the appearance of the movement) most contralateral forelimbs can be said to extend. Even the limbs of cats #XXVI at 500:1 and XXIII at both frequencies have a general appearance of extension of the limb, in spite of the flexed elbow (as explained earlier this flexion is minimal). On the same basis, most ipsilateral limbs can be considered flexed. This is consistent

with the findings of Thiele (32) and Hinsey et al. (8).

In relation to the constant extension of the wrist and toes, it is interesting to speculate on its relation to walking patterns. Such patterns have been obtained from the reticular formation in unanaesthetized animals by Sprague and Chambers (31) and this was believed to be the function of this part of the brain by earlier authors (32, 8). If the movements of a walking cat are visualised, it is immediately obvious that as it lifts its paw from the ground, it actively flexes the shoulder and elbow but that the wrist and toes are only passively flexed. They are even extended as the movement progresses to prepare the placing of the paw as the rest of the limb extends forewards. Active flexion of these two joints seem unnecessary in the normal walking pattern.

There is no simple parallel between those areas of the reticular formation which yield facilitation and inhibition and those which give specific postural patterns. Stimulation of the medulla by Sprague and Chambers (31) yielded ipsilateral forelimb flexion and contralateral forelimb extension in those areas giving inhibition of reflexes according to Magoun and Rhines (12), and the reverse was obtained in those areas yielding facilitation. One would therefore expect that the midbrain which yields facilitation (20) should give ipsilateral extension and contralateral flexion. This according to the work of other investigators (32, 8, 10), and our own, is evidently not so.

Changes in the nature of the movement with changes in frequency have not been reported by previous workers who stimulated the reticular formation. They have been observed here in five of the ten animals. Cats #XXVI, XXIV, XIX showed this difference in both limbs; XXV in the contralateral and XXI in the ipsilateral limb only. That this should not have been reported by previous authors is consistent with the results obtained here, i.e., the changes were found between 300 and 500 cps. Sprague and Chambers (31) used a maximum of 250 cps. It is true that the high frequencies used in this experiment are probably quite unphysiological but they do yield a change in movement.

Theoretically a nerve fiber can respond at a rate of 1000 cps. The synapse on the other hand cannot respond at such a high frequency. Various synapses have various maximal frequencies at which they can respond. Some cannot follow rates even as low as 20 cps while others can respond as fast as 500 cps (Hsiang-Tung Chiang, 9). Moreover, the degree of blocking effect of repetitive stimulation seems to increase with the number of synapses.

It would seem that some of the synapses concerned with the extension of the joints cannot respond as well to high frequency stimulation as those of flexion. This may be due to their own physiological characteristics or to the fact that extension is mediated by a pathway containing a larger

number of synapses. The latter explanation is believed to be the correct one for reasons to be discussed later together with the changes after the lesion.

The changes in movements with changes in frequency described here parallel the findings of Ranson and Hinsey (19) that rapid faradic stimulation of a sensory peripheral nerve sometimes called the contralateral flexor muscle into activity while lower stimulation rates gave pure crossed extension.

Similar changes though as yet unreported from reticular formation stimulation, have been known to occur from other areas of the central nervous system. Cure and Rasmussen (4) have shown how variations in the frequency permitted them to construct 3 cortical maps of somatic motor representation. At low frequencies the distal muscles were most easily affected; at high frequencies, the proximal. Such a selective effect upon distal and proximal muscle groups could not be obtained from the reticular formation. Indeed, even the order of appearance of the joint movements were the same at both frequencies used. The elbow appeared first, followed with increasing voltage by the shoulder and finally the wrist and toes.

The differences observed here after a change in frequency were a shift from a group of synergists to their antagonists. A more directly comparable variation with changes in frequency has been reported in 1950 by Moruzzi (17). He states that inhibition of decerebrate rigidity and of myotatic reflexes

is elicited by stimulation of the cerebellum at 50 to 300 cps, whereas facilitation results from rates of 2 to 30 cps. This has not been observed from the reticular formation of the brainstem. It would seem that the critical frequency is much higher from the latter area, and the results of this series of experiments suggest that a reversal of facilitation and inhibition might occur at about 400 to 500 cps.

2. Nature of the movements after the lesion.

After the postbrachial section, changes did occur in the patterns of muscular movement elicited by reticular formation stimulation.

This is an indication that these patterns are not present as such within the reticular formation of the midbrain, or do not depend solely upon direct reticulospinal pathways to the cervical cord. They must somehow be modified by other systems ascending from lower levels of the spinal cord to the cervical segment. How the latter systems exert their effect is a matter of speculation.

The hypothesis supported here is that reticulospinal fibers not only activate the cervical segments of the cord but also send impulses reaching lower levels which are then relayed back to the brachial segments to modify the original more direct effect upon the forelimb musculature.

First, we must consider the anatomical basis of this hypothesis. The term reticular formation was used by early anatomists to designate those parts of the medulla, pons and midbrain made up of cells scattered within the core of the brainstem, and surrounded by a network of fibers running in all directions. It has recently been shown that this so-called diffuse area is more precisely organized than had been suspected. On the basis of cytoarchitecture, it has been divided by Olszewski and Baxter (18) into a wide variety of nuclei. These may again be classified according to their afferent and efferent connections, although there is often a considerable amount of overlap between a number of nuclei (Brodal 2, Rossi & Zanchetti 20). One must distinguish three nuclei which project to the cerebellum and the rest which do not. The latter are again subdivided into a medial and a lateral group. The former gives rise to long afferent fibers projecting outside the brainstem, i.e., descending to the spinal cord or ascending to the thalamus, the subthalamus, the hypothalamus and to the basal ganglia. The lateral nuclei project unto the medial group through shorter axons.

The descending reticulospinal axons have been shown to originate from cells in the medial part of the reticular formation of the pontine and medullary regions only. They are concentrated in the nucleus reticularis gigantocellularis in the oral portion of the medulla, and in the intermediate part

of the pontine regions, (caudal part of the nucleus reticularis pontis oralis and rostral part of the nucleus reticularis pontis caudalis). The fibers from the pons are strictly ipsilateral; those from the medulla are bilateral though chiefly ipsilateral. They all end in almost equal number in the cervical and thoracic segments of the cord but stop short of the lumbar region. It has been suggested that the descending reticular pathways are continued as proprio-spinal fibers at this caudal level.

Although the midbrain reticular formation is the origin of some long ascending axons, (to the hypothalamus and basal ganglia with which it is reciprocally connected) it does not give rise to long descending fibers. However, the work of the Scheibels (24) demonstrates that the axons of the cells in this region do dichotomize into an ascending and a descending branch. Many of these do not project outside the brainstem and do not fit in the long fiber system category of Brodal. Neither can they be classified as Golgi type II. Indeed, in spite of the prevalent opinion, Golgi type II cells have never been found by these authors in the reticular formation of the brainstem. We may perhaps be permitted to refer to them as short fibers. However, the axons usually have collaterals ending in the vicinity of the cell body and dendrite. They have been referred to as the Golgi type II component of the axon system of the cells (24).

It is through these short descending axons and Golgi type II collaterals that impulses from the reticular formation of the midbrain can descend to the pontine and medullary reticular formation. The area of potential interaction of these dichotomizing axons has been described as a conical shaped mass with its long axis directed parallel to the long axis of the brainstem. This organization suggests that though impulses may be transferred medially along the parallel conical fields to the contralateral side of the brainstem, the main line of transmission is along the ipsilateral long axis of the brainstem.

The impulses yielding movements by stimulation of the midbrain reticular formation would be transmitted through this multisynaptic pathway in the midbrain (or one short descending axon may be sufficient) to the areas of the pons and medulla. At this level, similar systems may carry them to the spinal cord but direct long reticulospinal fibers would be available to carry them to the cervical segments of the cord. From the anatomical data reviewed above, it is apparent that this direct effect would be mostly ipsilateral although some direct contralateral effect from cells of the medulla would also obtain. Intrasegmental fibers at cord level may also be responsible for contralateral effects.

Impulses descending along this reticulospinal pathway do not end in the cervical cord. They descend as far as the lower thoracic level. From here they are propagated through the propriospinal system until the lumbosacral segments are activated. Firing into the interneuronal pool at this level will certainly activate the spinal border cells of Cooper Sherrington (3, 30) described in the introduction (page 4). Impulses from this pathway reach the contralateral side of the cervical segment of the spinal cord.

At least three groups of axons fire upon the interneuronal pool of the cervical region at the time of stimulation. Direct reticulospinal fibers, intrasegmental fibers and long ascending propriospinal fibers from the spinal border cells of Cooper Sherrington. Direct reticulospinal fibers to the ipsilateral side will have a more powerful effect than upon the contralateral side and by ricochet (since they are driven by these ipsilateral fibers) the reverse is true of the intrasegmental and spinal border cell fibers.

The position of the ipsilateral forelimbs therefore would seem to depend mostly upon activation of the interneuronal pool by direct reticulo spinal fibers. This effect which is weaker on the contralateral side should be strongly modified, facilitated or antagonized, by the intrasegmental, and Cooper Sherrington cells driven by the more powerful ipsilateral direct reticulospinal pathway. This would explain that the

changes after the postbrachial section are greater on the contralateral than on the ipsilateral side. As reported earlier, the changes after the lesion consisted mostly of flexion or at least of the acquisition of a flexor component by the usually extended albow of the contralateral forelimb, (and the extension of two that were previously flexed). The ipsilateral limb was unaffected in its usually flexed elbow. Two extended elbows however did flex after the lesion.

It might be argued that the extension of the contralateral (or ipsilateral) elbow is mediated through intrasegmental and/or spinal border cells. Removal of the latter eliminates the extension completely or partially (as in compound movements). The wrist and toes remain extended after the lesion and are therefore, if the hypothesis holds, due solely to the direct pathways or to the intrasegmental fibers and are not modified by the spinal border cell system.

The same types of changes were found with high frequency stimulation. As discussed earlier this was believed to be due to the different capacities of the synapses to respond to high frequencies of stimulation. It will be recalled that the hypothesis was put forewards, that a longer polysynaptic pathway might be involved, accounting for this difference. That this is the case is largely supported by the evidence of the changes obtained after the lesion. Physical removal of the longer multisynaptic pathway yields results of the same nature as the physiological ablation of the same path-

way by high frequency stimulation.

All that has been said for the elbow applies with signs reversed to the shoulder which was changed from flexion to extension after the lesion. However, the types of changes found with high frequency stimulation does not parallel those found after postbrachial section. A more complex organization must be involved.

The flexion of the elbow found after the lesion and the hypothesis based upon this fact is difficult to reconcile with the Schiff Sherrington phenomenon (22, 23, 30) in which the extension of decerebrate rigidity is enhanced by postbrachial section. All that can be said at the present time is that, since there is no evidence of extensor rigidity in the otherwise normal animal after postbrachial section, it is quite possible that the sign of the effect of Cooper Sherrington cells is reversed after a decerebration. Or again it may be argued that the tonic effect of these cells upon the spinal cord is not the same as that obtained by electrical stimulation through the reticular formation.

It is fully realised that this is not a complete explanation. The same problem exists in the interpretation on the mechanism of decerebrate rigidity itself. The usual hypothesis is that it is due to a release of function within the facilitatory areas of the reticular formation. Yet, there is considerable experimental evidence that electrical stimulation of this structure yields reciprocal effects.

The changes observed after the lesion may of course be due to an entirely different mechanism. Proprioceptive impulses from the hindlimb could modify the position of the forelimb through ascending sensory systems. However, since there is no obvious change in the pattern of the forelimbs as the hindlimbs begin to move, this seems rather unlikely. Moreover, the independence of the Schiff Sherrington phenomenon from sensory impulses of the hindlimb has been proven (22).

Another interpretation is that the changes after the lesion may be due to the general depression of the animal. The increased thresholds point to such a depression. It should especially be noted that the absolute voltages do not overlap in the normal and in the sectioned animal, in at least 3 cats. If the same voltage had been obtained in the normal cat, the same movements might have been reversed. This also seems unlikely. The violence of the response in the normal animal was never surpassed and rarely attained after the lesion, a sure indication that the effective amount of current used in the postbrachial preparations was rarely as great as that for the normal cat.

The idea defended here that patterns of movements obtained by stimulation of the reticular formation are set at least in part within the spinal cord rather than completely within the reticular substance itself, is additionally supported

by the observations on threshold values for the appearance of the joints in the normal cat.

The first joints involved with threshold voltages are the elbow and then the shoulder. The last to appear are the wrist and toes. If the pattern of movement obtained was set up within the reticular formation, this would imply that each electrode was closest to cells controlling elbow movements. By increasing the voltage, the current spread to cells governing shoulder and finally to those for the wrist and toes, which therefore would always be correspondingly far away from the electrode tip. This is highly improbable.

An alternative, more plausible explanation, is that the reticular formation unselectively activates the interneuronal pool of the gray matter of the cord. Whatever pattern of movement is contained therein will then be brought into action. The increasing voltage only activates a greater mass of the reticular formation. This in turn causes greater activity at the interneuronal pool level and brings more muscle groups into play according to the pattern it contains.

The hypothesis supported here has an interesting counterpart in the ascending system of the reticular formation. Mancia and Menlders (13, 14) have shown that the background activity in the cerebral cortex and subcortical relays is of importance in determining the sign of the effect of reticular formation stimulation on peripherally evokes responses at those levels.

3. The time relationships of the movements.

The time relationships of the movements have been thoroughly described at the frequencies of 500 and 50 cps. They are also shown to be part of a gradation in timings which was completely charted out from 25 to 5000 cps in cat #XXVII (Chart #I).

The findings are in perfect accordance with the time relationships described by Mihailovic and Delgado (16) and contribute additional information as to the time the effect can be maintained at various frequencies. The petering out of the effect at high frequencies corresponds to that observed by Gernandt and Thulin (7) for the phenomenon of facilitation and inhibition at low frequencies. The jerky movement described by Mihailovic seems but part and parcel of this petering out phenomenon. The maintenance of the response at low frequencies corresponds to the prolonged effects described by Delgado in 1959 (5).

The time relationships are not consistently altered after the postbrachial section. However, the time the limb is held at its maximally developed position (and the time for its return to normal) seem to be significantly increased after the lesion, in two cats. This would suggest that the petering out effect might not be due to fatigue or depression of the pathways but rather to an inhibitory action on the part of structures within the spinal cord. If this is so, the presence

of inhibitory fibers could be postulated within the caudal portion of the spinal cord. This would account for the petering out effect as well as for the Schiff Sherrington phenomenon.

# CHAPTER VI

## SUMMARY

1. Ten adult cats were stimulated with monopolar square waves through bipolar electrodes chronically implanted in the reticular formation of the midbrain, at 500 and 50 cps. In 6 of these, the stimulations were repeated after a post-brachial section of the spinal cord.

2. In the "normal" cats, forelimb movements obtained, consisted mainly of flexion of the shoulder and elbow with extension of the wrist and toes in the ipsilateral forelimb, and extension of the elbow, wrist and toes with abduction and a variable shoulder in the contralateral forelimb.

3. Differences in the movements at the two frequencies were occasionally observed. 500 cps seems to favor flexion, 50 cps, extension.

4. The first joint to appear at threshold is the elbow, followed or accompanied by the shoulder. The wrist and toes appear last and are always extended.

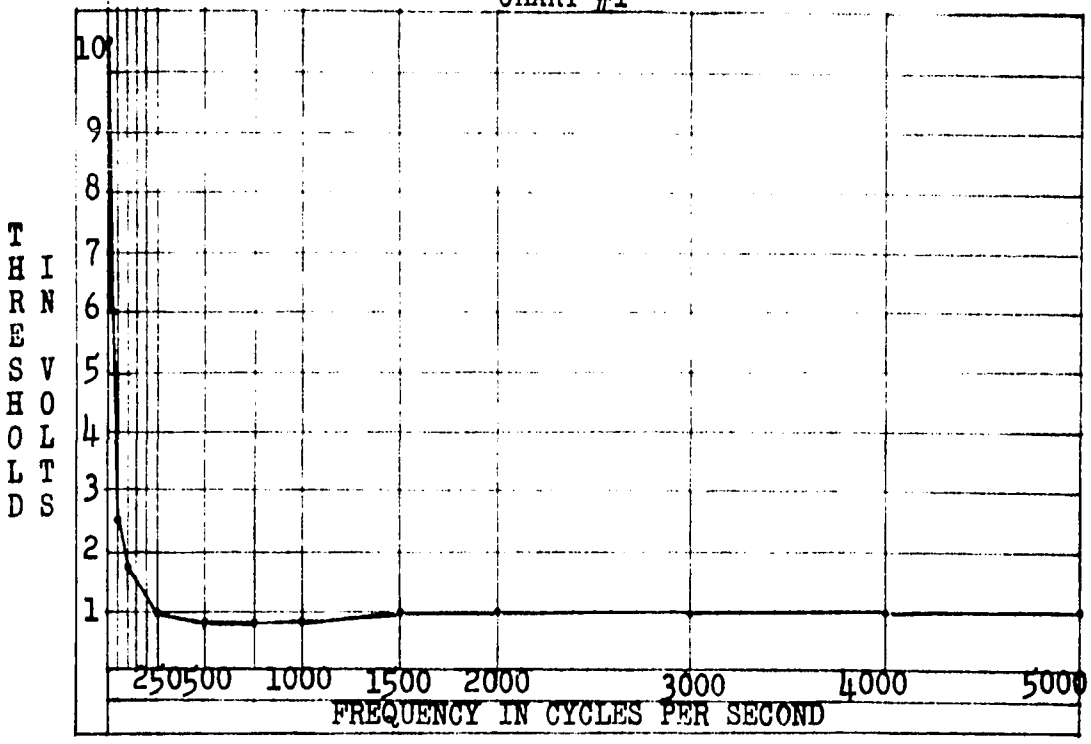
5. Postbrachial sections of the spinal cord favor flexion of the extended elbows in both forelimbs and extension of the flexed shoulder in the contralateral forelimb.

6. The time relationships of the movement are different at the two frequencies. 500 cps gives a quick movement which cannot be maintained at its maximal intensity for 20 seconds. 50 cps elicits a slow movement well maintained for the full time of stimulation.

7. The time relationships are not consistently modified by the postbrachial section. There is an indication, however, that the movement at 500:1 may be better maintained at its maximal development after the lesion.

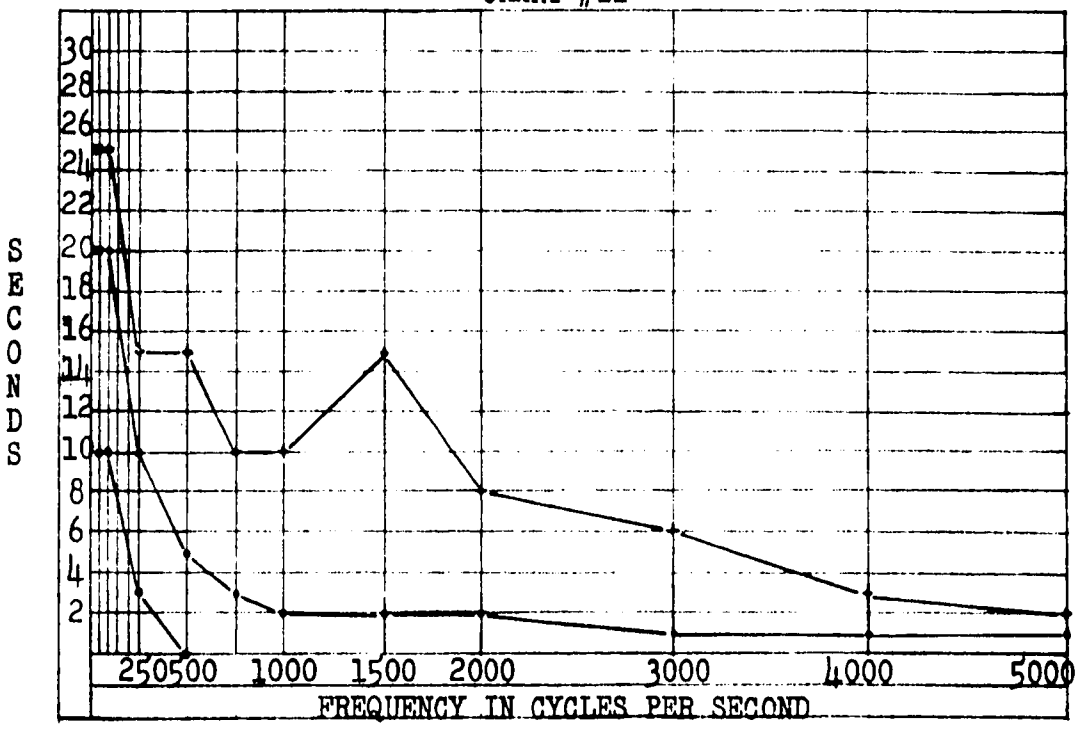
8. These results show that the forelimb movements obtained by stimulation of the reticular formation of the midbrain are, at least in part, dependent upon the intersegmental spinal cord organization. Extension of the elbow seems to be particularly influenced by pathways arising from cord levels below Th.4.

CHART #I




CAT #XXVII: Threshold voltages for pupil dilatation at various frequencies, with a constant impulse duration of 0.1 msec.

CHART #II




CAT #XXVII: Timings of the movements at various frequencies, with a constant impulse duration of 0.1 msec. Voltage for each frequency is 2.0v. above thresholds given in chart #I.
∘:maximal development. • :time of maximal effect. +:time to return to original position.

CHART #III

| CATFR: 50:5 | | | | | 500:1 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| # | JT: 1 | 2 | 3 | 4 | | 1 | 2 | 3 | 4 |
| XXVII | o | ● | ● | ● | abd | o | ● | ● | ● abd |
| XXVI | ● | ● | ● | ● | abd | o | o | ● | ● abd |
| XXV | ● | ● | ● | ● | abd | o | ● | ● | ● abd |
| XXIV | o | o | | | | | | | |
| XXIII | o | o | ● | ● | abd | o | o | ● | ● abd |
| XXII | o | ● | ● | ● | abd | o | ● | ● | ● abd |
| XXI | o | ● | ● | ● | abd | o | ● | ● | ● abd |
| XX | ● | ● | | | abd | ● | ● | | abd |
| XIX | | ● | | | abd | | | | |
| XVIII | o | ● | | | | o | ● | | |

CF MOVEMENTS

| CATFR: 50:5 | | | | | 500:1 | | | |
|---|---|---|---|---|---|---|---|---|
| # | JT: 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| XXVII | o | o | | | o | o | | |
| XXVI | o | o | ● | ● | o | o | ● | ● |
| XXV | o | o | ● | ● | o | o | ● | ● |
| XXIV | o | o | | | | | | |
| XXIII | o | o | ● | ● | o | o | ● | ● |
| XXII | o | o | ● | ● | o | o | ● | ● |
| XXI | o | o | ● | ● | o | o | ● | ● |
| XX | o | o | | | o | o | | |
| XIX | ● | o | ● | ● | o | o | | |
| XVIII | o | ● | | | o | ● | | |

IF MOVEMENTS

o:flexion ●:extension ◐:compound movement-flexion reversing to extension ◑:compound movement-extension reversing to flexion

N.B. When two rows are present, the top one represents a lower voltage, the bottom one, a higher voltage.

CHART #IV

| Movt | Limb: CF Freq: 50:5 | 500:1 |
|---|---|---|
| f12e34 | - | XXVI abd |
| | - | - |
| | XXIII abd | XXIII abd |
| | - | - |
| | - | - |
| f12 | - | - |
| | XXIV | - |
| | - | - |
| | - | - |
| fle234 abd | XXVII | XXVII |
| | - | XXV |
| | XXII | XXII |
| | XXI | XXI |
| fle2 abd | XVIII | XVIII |
| el234 abd | XXVI | - |
| | XXV | - |
| el2 abd | XX | XX |
| elf2e34 e2 abd. | - | - |
| | XIX | - |

PATTERNS OF CF MOVTS

| Movt | Limb: IF Freq: 50:5 | 500:1 |
|---|---|---|
| f12e34 | XXVI | XXVI |
| | XXV | XXV |
| | XXIII | XXIII |
| | XXII | XXII |
| | XXI | XXI |
| f12 | XXVII | XXVII |
| | XXIV | - |
| | XX | XX |
| | - | XIX |
| fle234 abd | XXVI | - |
| | - | - |
| | - | - |
| | - | - |
| fle2 | XVIII | XVIII |
| el234 abd | XIX (no abd) | - |
| | - | - |
| el2 | - | - |
| elf2e34 e2 abd. | - | XXI (Low ▼) |
| | - | - |

PATTERNS OF IF MOVTS

CHART #V

| CAT # | Normal JT:1 | 2 | 3 | 4 | Lesion 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|---|
| XXVII | o | ● | ● | ● | abd | ● | o | |
| XXVI | ● | ● | ● | ● | abd | ● | ● | ● ● abd |
| XXV | ● | ● | ● | ● | abd | ● | ● | ● ● abd |
| XXIV | o | o | | | | ● | | abd |
| XIX | | ● | | | abd | o | o | |
| XVIII | o | ● | | | | o | ● | |

CF MOVEMENTS
50:5

| CAT # | Normal JT:1 | 2 | 3 | 4 | Lesion 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|---|
| XXVII | o | ● | ● | ● | abd | ● | o | |
| XXVI | o | o | ● | ● | abd | ● | ● | ● abd |
| XXV | o | ● | ● | ● | abd | ● | ● | ● abd |
| XXIV | | | | | nil | | | |
| XIX | | | | | nil | | | |
| XVIII | o | ● | | | | back-fore | | |

CF MOVEMENTS
500:1

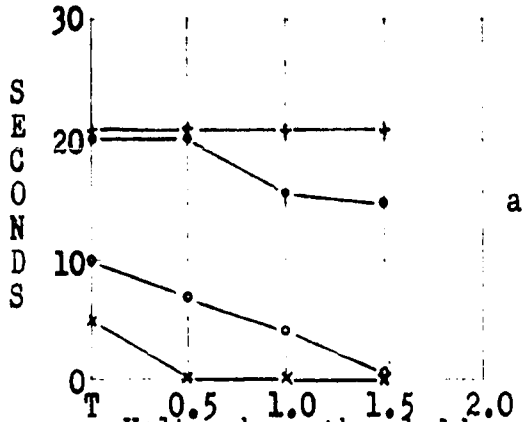
| CAT # | Normal JT:1 | 2 | 3 | 4 | Lesion 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|---|
| XXVII | o | o | | | o | o | | |
| XXVI | ● | ● | ● | ● | ● | ● | ● | ● |
| XXV | o | o | o | o | o | o | o | o |
| XXIV | o | o | | | nil | | | |
| XIX | ● | ● | ● | ● | o | o | | |
| XVIII | o | ● | | | o | o | | |

IF MOVEMENTS
50:5

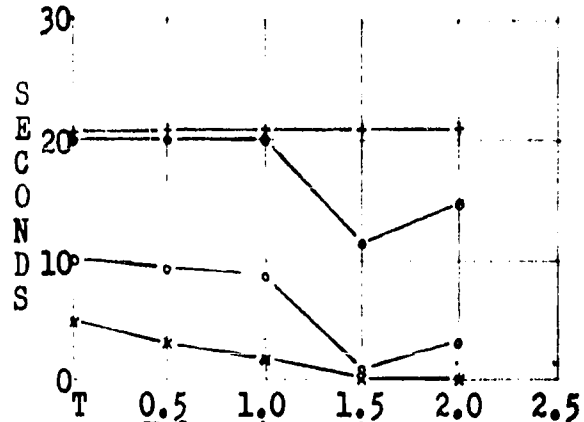
| CAT # | Normal JT:1 | 2 | 3 | 4 | Lesion 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|---|
| XXVII | o | o | | | o | o | | |
| XXVI | o | o | ● | ● | o | o | ● | ● |
| XXV | o | o | ● | ● | o | c | ● | ● abd-add. |
| XXIV | | | | | nil | | | |
| XIX | o | o | | | o | o | | |
| XVIII | o | ● | | | fore-back | | | |

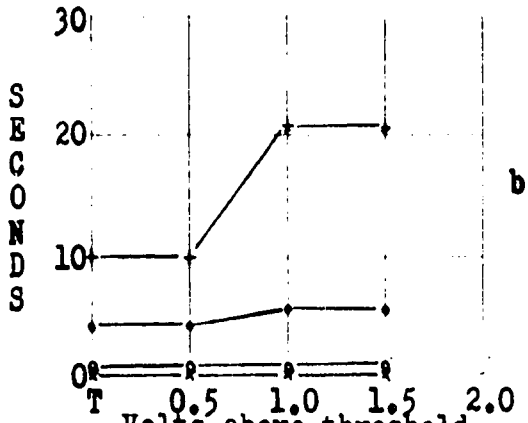
IF MOVEMENTS
500:1

o:flexion ●:extension o:compound movement-flexion reversing to extension ●:compound movement-extension reversing to flexion
N.B. When two rows are present, the top one represents a lower voltage, the bottom one, a higher voltage.

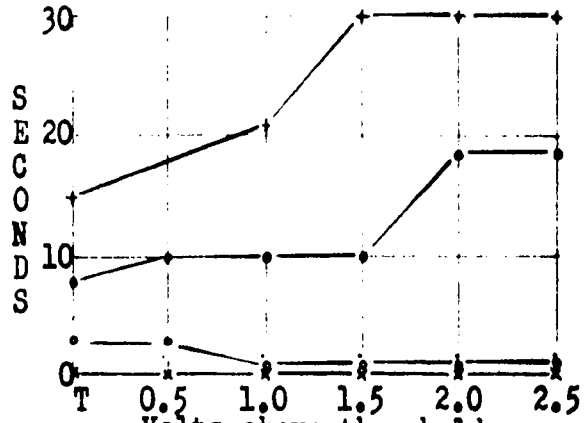


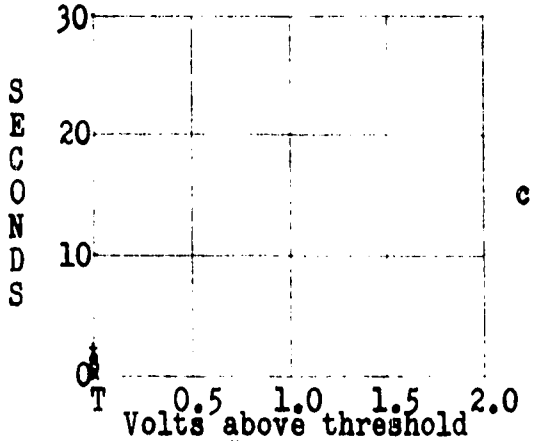

a)



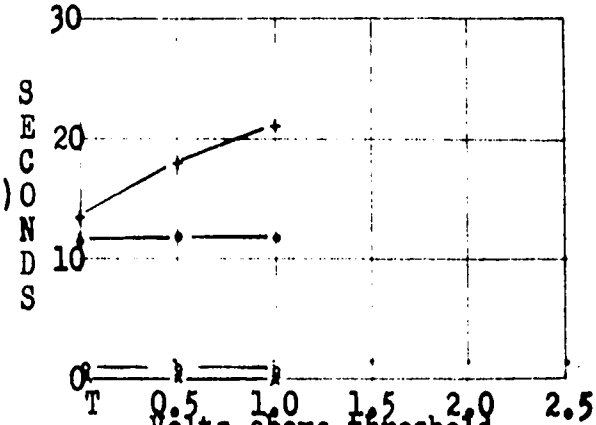




b)




c)




×:Latency •:Time position is held maximally

∘:Time to maximal development +:Return to original position

CHART #VI

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